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# A MANUAL OF HISTOLOGY

V. H. MOTTRAM

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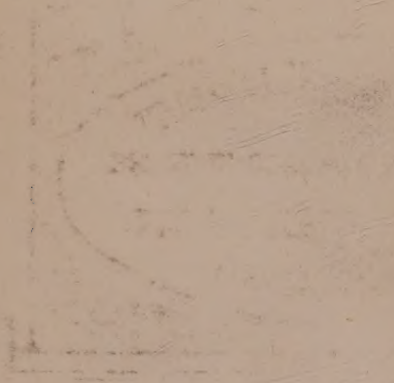

# A MANUAL OF HISTOLOGY

# A MANUAL OF HISTOLOGY

BY

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*First Published in 1923*

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PRINTED IN GREAT BRITAIN

TO
MY WIFE

# PREFACE

THE author has during the last eighteen years often wished for a book on histology with diagrams which he could set before a student who asked to be told what to look for under the microscope. Usually he has been forced to make a drawing there and then, for the best textbooks rarely have figures illustrating low- and high-power views of each tissue or using a convention at all like that of the student. He draws in line; the textbooks illustrate in line, or half-tone, or by photomicrographs, or by lithography. They never keep to one convention. This is confusing. Textbooks, too, have a habit of diverging towards the new, or the exciting, or the difficult, and leave the commonplace and ordinary on one side. But it is the ordinary and the commonplace which are essential to the student. He must know what a mammalian skeletal muscle looks like in longitudinal and tranverse section under ordinary powers, before he can (if ever he should) go on to the controversies concerning the mechanisms which histologists imagine they see in insect muscle under the highest possible magnification.

This book, then, is meant as a student's textbook, and an attempt has been made to give the student a clear diagram, using the same convention throughout, and that the one most students use, of every tissue and organ with which he is likely to meet in the histology laboratory. It is hoped that this book will save the student and the demonstrator much needless waste of time, and give them a chance of dealing with the less elementary aspects of their subjects.

But research and physiology could not be prevented from breaking in. No one can learn histology for its own sake. So free use has been made of any association, physiological or otherwise, as an aid to the student. The links between subjects, not their disunion, need emphasis to-day; integration must take the place of differentiation.

Acknowledgments are due to many persons for the loan of and permission to draw histological preparations. To Professor Sir Charles Sherrington for access to the cabinet of slides at Liverpool in 1912-13, to Professor Langley for similar access during the Long Vacation at Cambridge in 1921, to my colleagues Dr. Philippa Esdaile, Dr. Gladys Hartwell and Miss Clifford, and to my wife for the loan of slides and help in the work, my best thanks are given.

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*May*, 1923.

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# A MANUAL OF HISTOLOGY

## CHAPTER I

## HISTOLOGY AND THE CELL

### DEFINITION

HISTOLOGY is that branch of biology which describes and classifies the structures that go to form the warp and woof of an organism. The name is derived from ἱστός, a web or tissue, and λόγος, a word, or discourse. It is the science of tissues. And as the magnifying glass and the microscope are, *par excellence*, the implements which enable us to investigate the structure of tissues, histology is frequently described as microscopic anatomy. It is a branch of morphology (the science which deals with the shape of things), and though in Great Britain and Ireland usually taught in the schools of physiology, has really no intimate logical place in physiology, which deals with the functions and not with the shape and composition of organisms. Physiology makes an enormous use of the findings of histology, for shape often denotes function, and function determines shape.

Obviously there must be a plant histology and an animal histology, and also a histology of artificial fabrics made by man or other animals. And further, animal histology may be divided into a vertebrate histology and an invertebrate histology. We shall study vertebrate histology in the succeeding pages, though occasionally we may use invertebrate or even plant histology to illustrate a process present in vertebrates but not so readily demonstrable.

### METHODS USED

As stated above, our chief implement in histology is the microscope, either simple or compound, and we can vary the

magnification or the lighting at will with the instruments that are at our disposal to-day. For the technique of microscopy the specific textbooks on the subject must be consulted. For average work the student needs a microscope with a $\frac{2}{3}$ in. and $\frac{1}{6}$ in. objectives, and a No. 2 and No. 4 eyepiece. Occasionally he will need a $\frac{1}{12}$ in. oil immersion objective. These give, when compared with an object at the level of the table on which the microscope stands, roughly the following magnifications :

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| $\frac{2}{3}$ in. | objective. | No. 2 | eyepiece. | About | 87 | linear | magnification.[1] |
| $\frac{2}{3}$ ,, | ,, | ,, 4 | ,, | ,, | 147 | ,, | ,, |
| $\frac{1}{6}$ ,, | ,, | ,, 2 | ,, | ,, | 368 | ,, | ,, |
| $\frac{1}{6}$ ,, | ,, | ,, 4 | ,, | ,, | 620 | ,, | ,, |
| $\frac{1}{12}$ ,, | ,, | ,, 2 | ,, | ,, | 850 | ,, | ,, |
| $\frac{1}{12}$ ,, | ,, | ,, 4 | ,, | ,, | 1,500 | ,, | ,, |

Whenever possible magnifications should be known, and the drawings in this book have either the scale in microns (1,000 microns, $\mu = 1$ mm.) or the objectives and eyepieces used given with them.

The object of histology being to describe the appearance and structure of the tissues as they are when living, they should be, when possible, examined fresh, either *in situ* or mounted, and perhaps teased, in a solution that will not swell or shrink them (tissue juice, peritoneal fluid, isotonic salt or Ringer's solution) and will allow them to live long enough for observations to be made before post-mortem changes make their appearance. To aid in such observations, made under conditions of great difficulty, dyes which hardly damage the living cell, such as neutral red, methylene blue, or brilliant cresyl blue, may be added to the fluid in which the tissue is observed. Or again, the risk of post-mortem changes is taken, the tissue is killed, fixed, hardened, cut into thin sections and stained. Clearly this is drastic treatment, and again and again in the history of histology results have had to be discarded (e.g. Nissl's granules in nerve cells) because they have been produced by the method of preparation and were not present originally in the cell. Consequently the student of histology

[1] These figures were calculated from the writer's microscope, a Zeiss with A, D, $\frac{1}{12}$ in. objectives. They will be a little larger than the normal because the mechanical stage raises the objects farther from the table on which the drawings are made.

must be on his guard in accepting plausible preparations. Anything at all doubtful must be controlled by the appearance of the fresh tissue under the microscope with various lightings (oblique, dark ground, ultra-violet, etc.) or stainings (intravitally or otherwise). Histology is *not* the *art* of preparing striking specimens with various fixatives, mordants, and dyes, but the *science* of the analysis of tissues, using, when necessary, lenses and dyes.

## THE CELL THEORY

When an animal or plant tissue is teased or cut in thin sections and magnified, it is seen not to be simple and homogeneous. It is composed of unit structures called cells. The term " cell " comes from the appearance of the honeycomb, for the earlier tissues examined (e.g. elder pith) looked very much like a honeycomb. Gradually all tissues were found to consist of cells and the things laid down by cells. Sometimes the cell predominates, as in the liver, kidney, or salivary gland ; sometimes the cell is so obscured by the products of its own activity that it is difficult to persuade the beginner that it is there at all. This is so in tendon, or bone, and, to a less extent, in cartilage.

Not all animals, or all parts of an animal, have clear divisions between the units, but in the animals usually studied by students of physiology the divisions between the cells are fairly sharp. Thus the cells of the secretory glands, such as salivary glands, can easily be made out (cf. fig. 101). It is only in such things as the slime fungi that there are no lines of division between the cells that fuse to form them, so that we can hardly say whether there is only one organism present or a community of organisms fused into one. But this problem rarely arises, and it may be left to zoologists to decide whether the slime fungi are one organism or many. Whether the amœba is a unicellular or a noncellular animal, and whether it or any infusorian or bacterium should be considered comparable with a human being, or with one of the cells in a human being, are moot points. The bias of the physiologist is toward the former, and to him animals are simply cellular or noncellular.

*It is essential that the student of histology should learn to recognize at a glance the manifold elements of a tissue.* Unless

this is done there is no possibility of understanding histology, nor is any work in physiological, pathological, or bacteriological histology possible. Man, and most animals that we study, consist of cells, and to understand their structure, whether normal or pathological, you must master the appearance of the cell and its manifold and wonderful variations.

## THE CELL OF CELLULAR ANIMALS

The cell is Protean in its shapes and sizes. Any one secretory cell of (say) the human parotid gland is much like any other (fig. 99). But it differs from a secretory cell of the human pancreas. The secretory cells of the human liver have subtle differences that distinguish them from those of a monkey or of a pig. These differences are, perhaps, shadows of shades (at any rate to the beginner), but the differences between cells of the different parts of the body, or different animals, are enormous. Thus the human ovum (egg cell) is only just visible to the naked eye, while that of the hen (the breakfast egg) may be two inches long, and that of the ostrich, six. Some nerve cells are about 5$\mu$ (i.e. five thousandths of a millimetre) long; while others stretch from the cortex of the brain, right down to the lumbo-sacral regions of the spinal cord. This variability is somewhat staggering, but by classification it is simplified, especially when it is understood that this difference in form is due to a difference in function. No cells that have different functions have quite the same form. Enormous specialization has occurred among the cells of the "higher" animals, and when a cell specializes it takes on a specific shape. Some cells secrete, others move parts of the body, others carry messages, and so there is diversity of form. The morphology of the cell varies with its physiology, and so a knowledge of the form of the cell aids in the understanding of its physiology, and if the cell be working wrongly, of its pathology.

## THE TYPICAL CELL

To crystallize an idea of the cell it is best to take a relatively simple cell, but one, nevertheless, containing many of, if not all, the structures to be found in cells. For this purpose the liver cell, though small, is convenient.

The liver cell is a polyhedral, roughly cubical, cell of about

20$\mu$ (20 thousandths of a millimetre) across. It varies considerably in shape according to its particular neighbourhood, juxtaposition to other cells, etc. Teased from a freshly killed animal in tissue juices, or abdominal fluid, and viewed under a good magnification (say 600 or with a $\frac{1}{8}$ in. objective and a 4 eyepiece) it is seen to consist of two main things: (1) a mass of fairly clear protoplasm in which are shining, and somewhat refractive granules or globules of two or more kinds; and (2) one, or more, spherical nuclei. The protoplasm of the cell, to distinguish it from that of the nucleus, is usually called cytoplasm (i.e. cell plasm); that of the nucleus, karyoplasm (i.e. "nut" or nucleus-plasm). Whether the cell plasm has any structure or not has been the object of violent controversy, but the present generally held opinion is that it is fairly homogeneous, with important "elements" embedded in it (i.e. granules, chondriosomes, crystals). These elements are doubtless extremely important in the history and the functions of the cell. They may be (1) chondriosomes,[1] minute bodies, found by means of special staining during the life of the cell, which apparently preside over the manufacture of the storage products or the substances to be secreted by the cell; (2) storage products, or (3) products that are later turned into secretions. All such are to be seen in the liver cell, though with difficulty in any one cell. The small granules seen in the fresh liver cells are the chondriosomes, and can be fixed and stained by appropriate methods. The large spherical globules are fat (a storage product). Small black globules, sometimes seen, are iron-containing, and represent an activity of the liver cell which is to reserve the iron of the hæmoglobin (the red colouring matter of the red corpuscles) of effete red blood corpuscles, and secrete the rest in the *bile*. From the liver of a well-fed dog or rabbit large quantities of a carbohydrate called glycogen can be extracted, which stains mahogany red with weak iodine.

If you irrigate a section of such a liver under the microscope with weak iodine solution, the same red develops in granular masses; clearly this is glycogen, a storage product. So the liver cell is fairly characteristic in that its cytoplasm is granular and that these granules may be (1) chondriosomes, (2) storage products (fat and glycogen), and (3) substances having to do with secretion. The reader is referred to figs. 108, 110, 111,

[1] Alternative name: mitochorndria.

and 113 in the section on the liver, and to fig. 102 for secretory granules.

The nucleus of a freshly teased liver cell is a disappointing object. Little structure can be made out in it by ordinary illumination. It is a spherical translucent object, nearly homogeneous. But we are justified in assuming that it is like the nuclei of other cells because, when stained, it appears to have structures similar to theirs. When the nucleus of a fixed and stained liver cell is observed, a delicate chromatin network

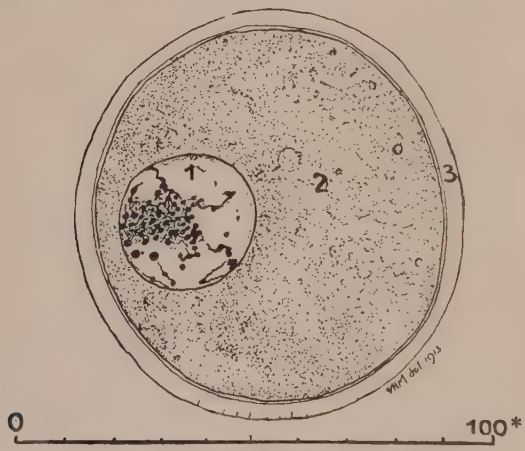


FIG. 1.—Ovum of Guinea Pig.

1. Nucleus showing sharply stained chromatin. 2. Cell plasm, or cytoplasm, containing a dust of fat particles. 3. Cell membrane.

with large knots at the junction of the threads is seen, and a fairly large shining object, spherical in shape—sometimes there are two or three of them—is also observed : the nucleolus. There should be no difficulty in observing chromatin when once you know what to look for. If the student finds any difficulty he should examine a well-fixed and stained preparation of an ovum (fig. 1), where the nucleus is large and the chromatin undoubted. The function of the nucleus is certainly to preside over the activities of the cell. *If you vivisect a cell, and cut any part away from the nucleus, that part dies.* (See nerve cell, Wallerian degeneration.) Cells without nuclei

* Except where otherwise stated the figures of the scale indicate microns ($\mu$) or thousandths of a millimetre.

(e.g. mammalian red blood corpuscles) rapidly die. The nuclei of vigorous, active cells stain deeply. If the cell is effete they stain poorly. So the staining of the nucleus is an index of its state.

From these considerations we can build up a hypothetical idea of a cell of which a diagram is given. It has :

(*a*) Cytoplasm containing (1) chondriosomes ;
(2) granules which may be storage products or products for secretion ;

(*b*) A nucleus (or nuclei) with its nuclear network and nucleolus (or nucleoli).

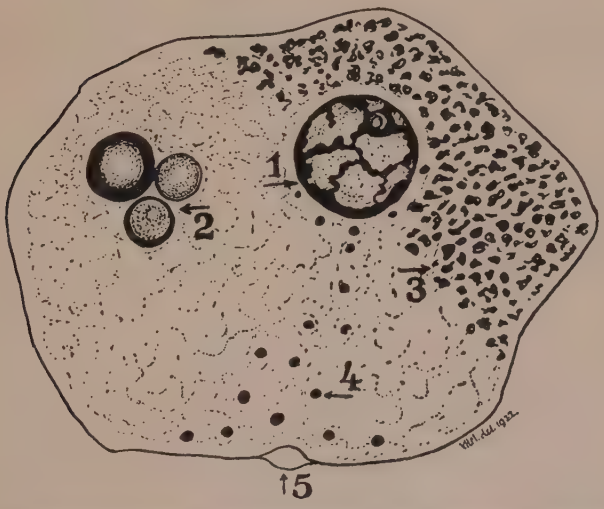


FIG. 2.—Hypothetical cell showing storage and secretory products based on the liver cell.

1. Nucleus showing chromatin and nucleolus. 2. Fat globules. 3. Glycogen. 4. Secretory granules. 5. Secretory channel.

Near the nucleus is found in some cells a small granule, the centrosome. Its function will appear later.

**Nuclear Material**—As said above, nuclei contain a network which stains with appropriate dyes. The dyes usually used (e.g. methylene blue or hæmatoxylin) are salts in which a colour-bearing part is the basic part of the salt. These unite with acidic substances, and it is assumed that the nuclear material which is stained is acidic. Such a substance obtains

the name of *chromatin* (i.e. colourable stuff). But throughout the nucleus is material which stains with acidic dyes. We know most about the chromatin, its occurrences and changes, and assume that the remainder follows the same course. Chromatin varies in amount and disposition in different cells. Thus the pancreas has the chromatin of the nucleus gathered up into one or more large particles, whereas in the parotid gland (which closely imitates it) the chromatin is more scattered throughout the nucleus (cp. figs. 99 and 104).

In young cells the chromatin is deeply stained and much in evidence.[1] (See the cells at the inner growing edge of the stratified epithelium in skin, œsophagus, bladder—figs. 25, 26, 170, 171, 188.) As cells become more effete the chromatin grows scanty and stains with difficulty (as in the upper layers of such an epithelium). The difficulty of showing much chromatin in the nuclei of nerve cells and liver cells must not be taken, however, as a sign that these cells are relatively effete. It is characteristic of these cells to have but little demonstrable.

But above all, it is in the dividing cell that the chromatin stains heavily. Wherever in a section you have heavily stained nuclei (see e.g. marrow, lymph glands, spleen, testis) you may be almost certain that there is active multiplication of cells in process. Various parts, even of the adult body, are actively growing, i.e. new cells are being produced. E.g. there are about $25 \times 10^{12}$ (25 million million) red blood corpuscles in the body, and the life of them may be at most three weeks, i.e. these have to be replaced at least every three weeks. Similarly the epidermis, the hairs, the nails, the white corpuscles, and the sperm have to be replaced frequently. This is done by the active division of cells at the seat of the growth. (See figs. 24–26, 187, 188, 134 and 135.)

## CELL DIVISION

The cell divides in one of two ways. Either the nucleus goes through the complicated process of mitosis (or karyokinesis), or it simply splits into two. The former is the common way and is to be described at length. The latter appears to take place in the epithelial cells of the bladder, the giant

[1] This is of practical use to the student, who can save himself the common mistake of thinking an epididymis is a testis. The testis has cells rapidly dividing and the epididymis none.

cells of the marrow, and in polymorphonuclear leucocytes (q.v.), but it is difficult to be sure that a rapid mitosis has not taken place. Such divisions are called amitotic.

## MITOSIS, or KARYOKINESIS

In between the resting stage of the mother nucleus and the fully formed daughter nuclei intervene changes that are, for convenience, divided into eight stages: four stages, the *anaphase*, leading to the division of the elements into which the chromatin breaks (chromosomes), and four stages, the *kataphase*, leading from this to the production of daughter nuclei.

(I) The centrosome divides, often before any change is seen in the nucleus, and lines (? strains in the protoplasm) appear, joining the daughter centrosomes, somewhat like the lines of force around two unlike magnetic poles. The centrosomes move farther and farther apart, *around* the nucleus, till they are, as it were, its north and south pole. A spindle appearance is thus formed (fig. 3).

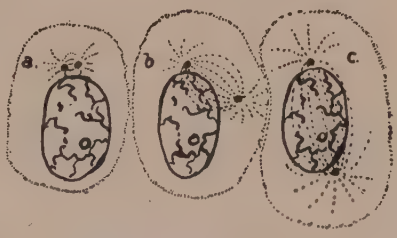


FIG. 3.—First stage of mitosis, division of the centrosome and formation of the achromatic spindle. The cell outline is dotted.

(II) The chromatin loses its net-like appearance and becomes one long twisted thread. (The spirem stage—fig. 4.)

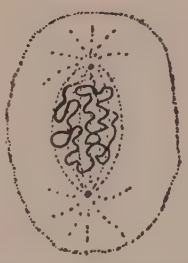

FIG. 4.—Second stage. The chromatin of the nucleus is now one long thread or spirem.

(III) The long thread breaks into a number of chromosomes of equal length, constant in number for any one species[1] (fig. 5).

FIG. 5.—Third stage. The chromatin skein has now broken up into an even number of segments, called chromosomes.

[1] Ascaris, 2; man, onion and salamander, 24, etc.

FIG. 6.—Fourth stage. End of Anaphase. The chromosomes have arranged themselves in the plane of the equator. [Monaster.]

FIG. 7.—Fifth stage. Beginning of Cataphase. Each chromosome has split longitudinally into two.

FIG. 8.—Sixth stage. The divided chromosomes leave their twin halves and migrate to opposite poles—the centrosomes. [Diaster.]

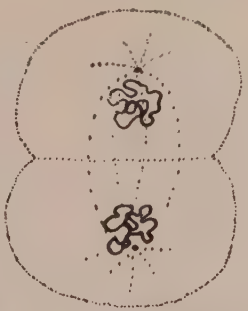

FIG. 9.—Seventh stage. Each group of twin chromosomes reconstitutes a skein or spirem. The cytoplasm of the original cell now begins to divide.

FIG. 10.—Eighth stage. Each spirem forms a nucleus and the cell division is completed.

(IV) These chromosomes arrange themselves (usually in V shapes) equatorially around the axis formed by the spindle. Because this looks like a single star, it is called the monaster stage (fig. 5).

(V) Each chromosome now splits longitudinally into two (fig. 7).

(VI) The split chromosomes move off to the poles, one half to one pole and one half to the other. As they now look like twin stars, this stage is called the diaster stage (fig. 8).

(VII) The chromosomes at each pole unite to form two spirems (fig. 9).

(VIII) Each spirem, by throwing out side branches, takes on the appearance of a new nucleus, the cell plasm now divides, and two daughter cells, each with a resting nucleus, are now complete (fig. 10).

Of course the various stages are continuous, and so can be divided into many more according to taste. Sometimes, too, the centrosome divides later during the spirem stage. Further, the spindle is not always

easily visible, nor are the centrosomes. In fig. 11, the centrosomes and the achromatic spindle were invisible—(larval salamander skin, one of Flemming's original preparations)—but are very clear in the ascaris ovum (fig. 12), as indeed they usually are in sex cells. (See Testis, fig. 135, p. 152.)

Mitotic figures are unusual in the ordinary preparations

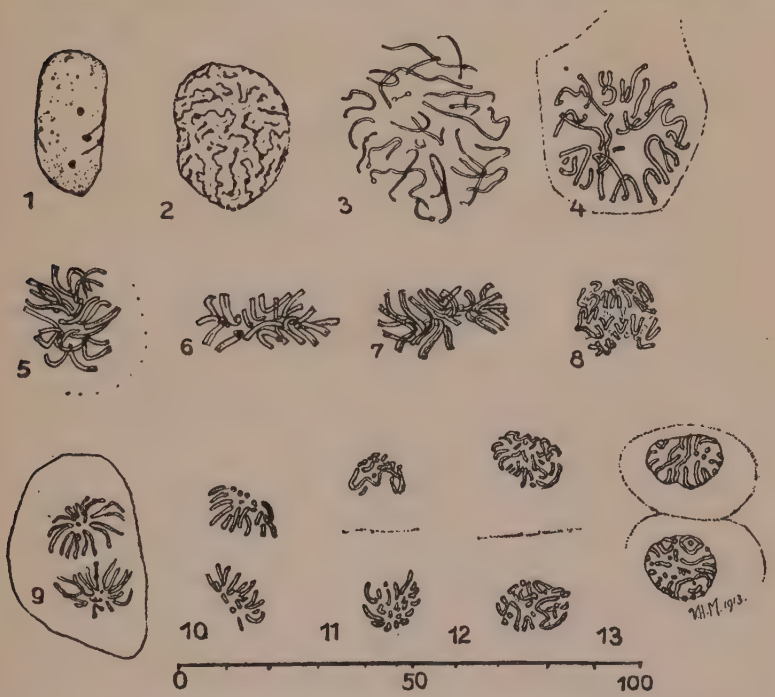


FIG. 11.—Mitotic figures from skin of larval salamander. Drawn from one of Flemming's original preparations.

1. Resting nucleus. 2. Early spirem formation. 3. Formation of chromosomes. 4 and 5. The chromosomes are beginning to split. 6 and 7. The chromosomes are arranging themselves equatorially. In 7, the longitudinal splitting is nearly complete. 8. The chromosomes are moving towards the poles. 9 and 10. Diaster stage. 11 and 12. Reconstitution of the spirem. 13. The formation of two daughter nuclei and cells is complete.

studied by medical students, except in fœtal tissues and tissues such as bone marrow, lymph glands, and testis, where actual proliferation is taking place. But they are visible in malignant growths (cancer), and also in red blood cells after extensive destruction of red blood corpuscles, and should always be looked for.

The function of mitosis is clearly to ensure that an equal amount of nuclear material of identical quality should go to each daughter cell, and it is not too much to see in them the mechanical basis of heredity, each chromosome carrying so much in the way of inherited characteristics. The constancy of the number of chromosomes is remarkable. In the sex cells half the chromosomes are extruded in an early division, otherwise in the fertilized ovum there would be twice the correct number, and therefore twice the number in all the cells that descend from it. The only exceptions to the rule of equality in the number of chromosomes is: (1) in some invertebrates in which the number of chromosomes is odd, i.e. $2n + 1$, and not even, $2n$, and so some sex cells get $\frac{2n}{2} + 1$ and some $\frac{2n}{2}$, and (2) in cancer cells where there is often gross irregularity in the partition of the chromosomes, some cells receiving more, and others less, than their share. It is thought that the halving of the chromosomes in sex cells, in addition to making the necessary reduction in the number of chromosomes, opens the way for *variation*, while the partition of the nuclear material between two daughter cells, determines *hereditary type*. The only difficulty involved in the latter is that nerve cells (say) and epidermal cells originally came from the same cell, and yet they have diverged enormously. This, fortunately, is a problem more for the zoologist than for the histologist.

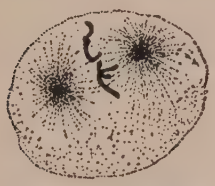

FIG. 12.—Dividing ascaris ovum.

## CHAPTER II

# THE ELEMENTARY TISSUES

TISSUES can be distinguished from one another by (*a*) the shapes, sizes, arrangements, and contents of the cells themselves, or by (*b*) the material laid down by the cells outside themselves. For convenience sake (the classification is not quite logical) tissues can be classed as (*a*) epithelial, (*b*) connective, (*c*) muscular, and (*d*) nervous. It is essential for the student to master these—a task that appeals to him less than that of identifying specimens—for the nature of an epithelium, or a connective tissue, or the arrangement of these tissues, will ensure an identification that otherwise would be false if based on the general appearance. No one who knows his types of epithelia and connective tissues can mistake a villus of the small intestine for those in the Fallopian tube, or a prostate for a mammary gland, or both for the thyroid or lung. Such wild identifications are common with students. It is especially essential in pathology to be able to recognize individual cells, for, in metastases of cancer, they may be in a totally different part of the body from that in which they originated.

Organs, such as the small intestine, may have each of the elementary tissues represented; in others, e.g. the central nervous system, three out of the four are present; in others, two only; while in some organs, or structures, we may have one so predominant as to appear pure. Connective tissue must, as its name implies, be present in every organ of the body. It is from the constitution of an organ, the types of tissue that go to form it, and from the shape and arrangement of the elementary tissues, that we recognize it for what it is.

## EPITHELIA

These are the simplest, perhaps, of the elementary tissues, for the extracellular material is reduced to the minimum.

Epithelia are found covering the whole body (with modifications where hair and nails are concerned), lining the whole of the alimentary and respiratory tracts, including sinuses, the uro-

FIG. 13.—Pavement epithelium (epithelioid membrane) of nerve sheath. The cell outlines are made visible by silver nitrate. $\frac{1}{8}$" × 2. C.

genital tracts, all secretory glands and their ducts, the ventricles of the brain and the neural canal, and the cavities of the internal ear. We may include, too, the epithelioid membranes of the mesentery, tendon, and nerve sheaths, of pleural and abdominal

cavities, and of the innermost lining of blood vessels and lymphatics.

Epithelia may be divided according to the number of layers of cells they contain into (1) simple and (2) compound. The former contain one layer of cells and are divided according to the form of the cells into (*a*) *pavement*, (*b*) *cubical and subcubical*, (*c*) *columnar*, (*d*) *ciliated*, and (*e*) *glandular*; the latter (compound) into *transitional*, those that contain two to four layers of cells, and *stratified*, those that contain more.

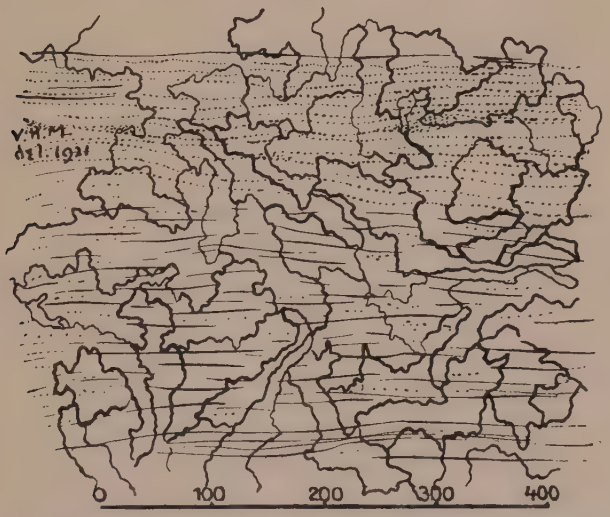


FIG. 14.—Pavement epithelium (epithelioid membrane) covering a tendon. Outlines of cells stained with silver nitrate. Tendon fibres dimly seen under epithelium. $\frac{3}{8}'' \times 4$. C.

**Pavement Epithelia** (Endothelia) or **Epithelioid Membranes**—These consist of very thin cells set edge to edge to form a mosaic tessellated pavement-like structure. They are best made out by means of silver nitrate, which forms a compound with the cement-substance between the cells and is reduced to metallic silver in sunlight. The deposit marks the outlines of the cells mainly, but may also appear wherever there are chlorides in the cells. The outlines of the cells are often very wavy and the crenelations fit into one another (figs. 13 and 14). In other preparations they may be wavy only (see fig. 15), or even diamond-shaped (fig. 16). The cells may

measure as much as 200$\mu$ in length (sheath of tendon and nerve, mesentery), but in blood vessels and lymphatics they are very much smaller (40–75$\mu$). The nuclei, which usually

FIG. 15.—Pavement epithelium (epithelioid membrane) covering the mesentery. Outlines of cells stained with silver nitrate. In addition some cells, especially the false stomata (*a*), show considerable staining within the cell, possibly owing to the presence of chlorides. $\frac{1}{8}''$ × 4. C.

are oval, must ordinarily be demonstrated by staining with a basic dye: the silver, if the treatment be prolonged, settles around them and not in them. Pavement epithelia are seen lining all blood vessels, including the chambers of the heart,

all lymphatic vessels, all serous spaces, Bowman's capsule (see fig. 121, showing endothelia of artery, capillaries, and Bowman's capsule), the alveoli of the lungs, and the surfaces of the tendons and of the nerves. The function of these frail and delicate membranes seems to be to present a distensible elastic membrane (blood vessels, especially in capillaries, and in Bowman's capsule) that shall be frictionless (blood vessels, serous spaces—pleura and abdomen) and present as little as possible

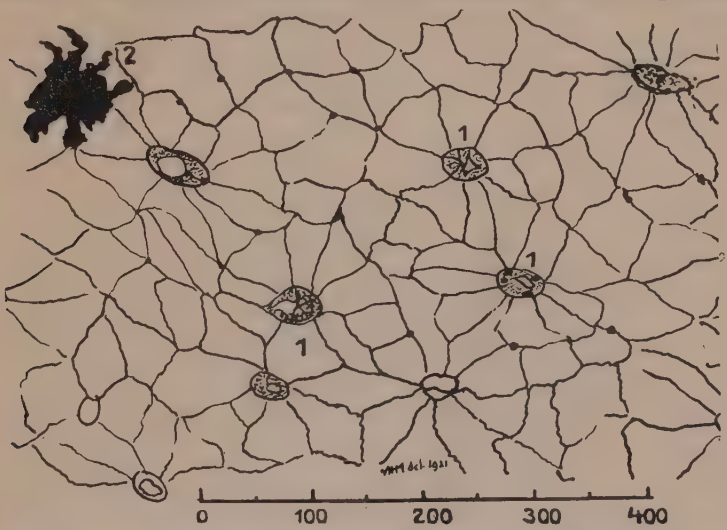


FIG. 16.—Pavement epithelium covering serous cavity. Silver nitrate. $\frac{2}{3}$″ × 4. C.
1, 1. Stomata. 2. Pigment cell.

resistance to the transference across it of fluid and the solutes contained in fluids.

**Cubical Epithelia**—These consist of a single layer of approximately cubical cells, usually lining a duct of a gland or an alveolus.[1] The nucleus is spherical and occupies a large portion of the cell. It usually stains deeply, or, if not, homogeneously. Cubical epithelium is to be found in the ducts of the salivary glands (figs. 100, 102), in the kidney (figs. 122 and 123), and of the liver. The epithelial lining of the alveoli of the thyroid gland (figs. 142, 143) consists of cells that are sometimes not quite so tall as broad, and is therefore

[1] Alveolus means a little hollow space. It is the unit structure in a gland. See p. 101.

termed "subcubical." See also inactive mammary gland, fig. 139. The regularity of cubical epithelia—the cells being identical in size, and the nuclei regularly spaced—gives it a characteristic and unforgetable appearance.

**Columnar Epithelia**—When the cells composing an epithelium are considerably taller than they are broad, the epithelium is termed columnar. Columnar epithelia are found in the mouths of the glands at the cardiac end of the stomach (figs. 95 and 97), throughout the pyloric glands (figs. 91 and 92), covering the surface of the villi of the small intestine (figs. 17, 175 and 176), and forming the glands of Lieberkühn and the tubular glands of the large intestine.

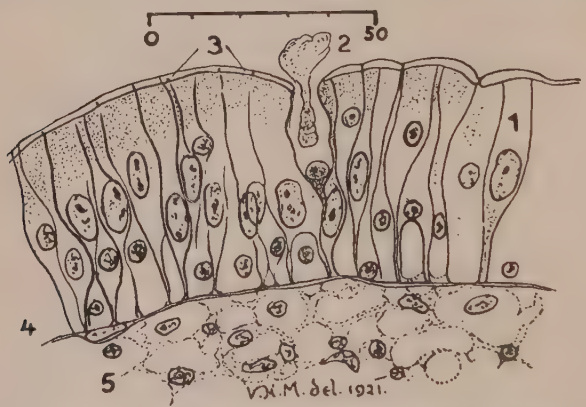


FIG. 17.—Columnar epithelium from villus of small intestine. Osmic. $\frac{1}{8}''$ × 4. C.

1. Columnar cell. 2. Goblet cell extruding mucus. 3. Striated border: striæ, however, not visible. 4. Basement membrane. 5. Reteform tissue.

There is some variation in the heights of the cells lining the ducts of the salivary gland and the bile ducts, and so these epithelia are often classed with the columnar epithelia (figs. 102 and 109).

The most typical columnar epithelium is found on the villi of the small intestine (fig. 17). Here the cells are some 40–50$\mu$ in height, with, at the most, a width of 10$\mu$. The cells are of two types: (*a*) cells with an oval nucleus and a well-marked upper border (often striated). These cells are often slender with a tapering foot. The nuclei are not all at one level, for they cause the cell to bulge slightly, and so one cell has its nucleus at a different height from the next. If the section is not very thin, the appearance—judging by

the nuclei—of an epithelium two or three cells deep is obtained. Granules are frequently seen in the cytoplasm, and if the

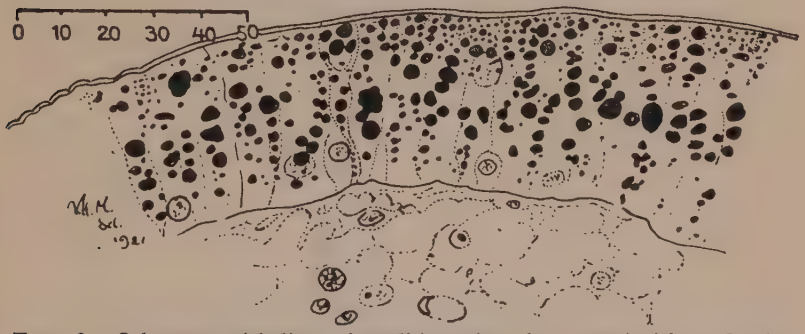


FIG. 18.—Columnar epithelium of small intestine after a meal of fat. Osmic. The fat globules are stained black. $\frac{1}{8}$″ × 4. E.C.M.

intestine has been absorbing fat, globules of fat are seen in these cells (fig. 18). (*b*) Goblet cells. These are cells fairly accurately described, in one of their phases, by their name. Their function is to secrete mucous material, and as they are continually manufacturing mucus, and then discharging it, cells in all stages of activity are seen in a single preparation. The cells are cylindrical, much like the ordinary columnar cell, with a round to oval nucleus. Mucin, or rather a precursor, is laid down in the cell *above* the nucleus. This part absorbs water, the granules of mucigen swell, and the cell perforce becomes goblet-shaped. The nucleus is pressed down against the foot. The distension increases and the cell bursts, discharging its mucin. In fig. 17 a cell is seen which has just

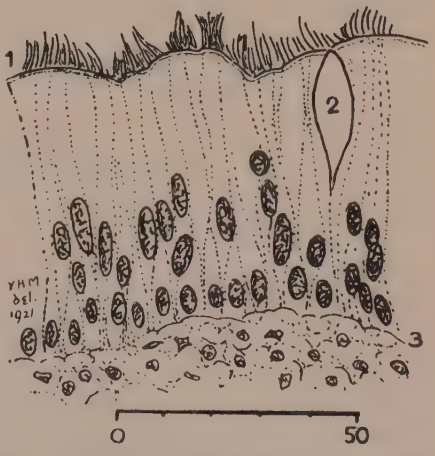


FIG. 19.—Ciliated epithelium from trachea. $\frac{1}{8}$″ × 4. E.C.M.
1. Cilia. 2. Goblet cell. 3. Basement membrane.

burst and is discharging its contents. When these have gone the cell regenerates, lays down mucigen granules, and the cycle recommences. Such goblet cells are also found in ciliated epithelia (see fig. 20). They are found in greatest

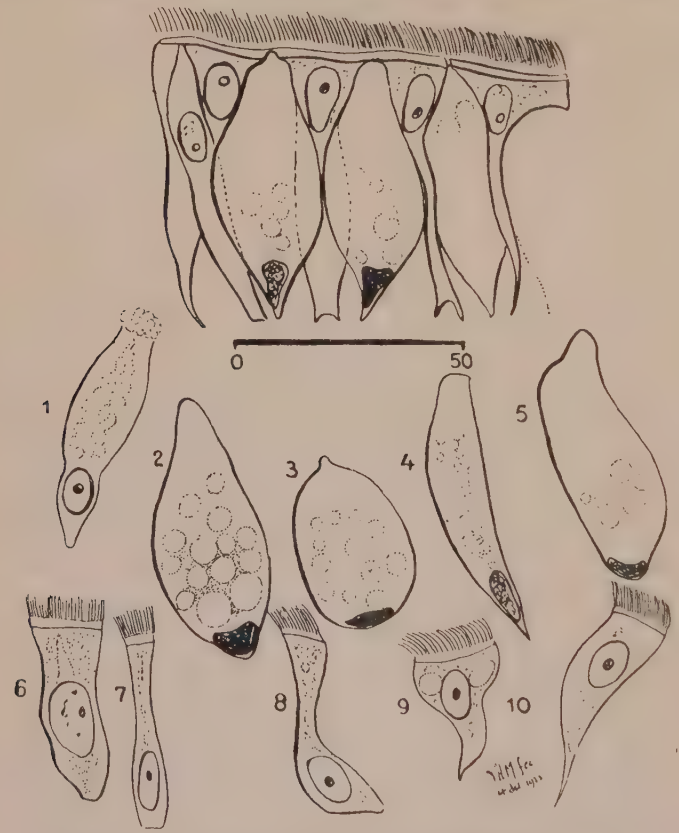


FIG. 20.—Ciliated epithelium (frog's mouth). $\frac{1}{6}$" × 4.

Above, epithelium with the ciliated and goblet cells *in situ*. Below, teased cells from the same epithelium. 1. Goblet cell immediately after extrusion of mucus. 2–5. Goblet cells in various stages of the production of mucus. 6–10. Various ciliated cells.

abundance in the glands of the large intestine, where practically every other cell is a mucous cell (see figs. 89 and 90).

**Ciliated Epithelia**—If we imagine the cells of columnar epithelium to acquire cilia,[1] we get a very good idea of what ciliated epithelium is like. There is a thinner striated border

[1] Thread-like, curved and motile projections of the cell. Cilium = an eyelash.

to the cells, and above this arise the cilia. The length of the cilia is approximately 7–10$\mu$ (see fig. 19). The preservation of cilia is not easy, so that the student often sees little more than a ragged edge in the various organs where they occur. The cilia run together and form a tangled mass. But it is possible to obtain isolated ciliated cells by scraping ciliated mucous membranes, teasing, and fixing carefully. (See figs. 19 and 20.)

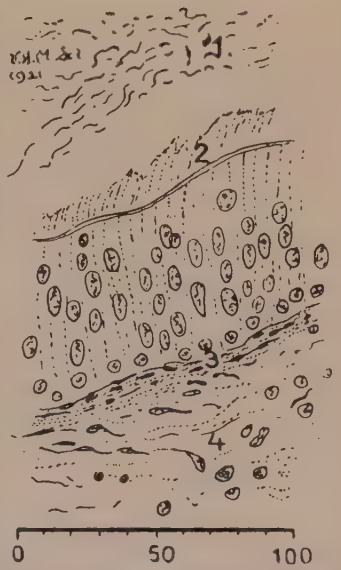


FIG. 21.—Epithelium of epididymis. $\frac{1}{6}$″ × 2. C.

1. Spermatozoa. 2. Cilia said not to be vibratile. 3. Basement membrane. 4. Connective tissue.

Goblet cells are found in abundance, in the passages lined by ciliated epithelia. These are: (1) The respiratory passages (excluding mouth, pharynx, upper part of glottis, and vocal cords), including the diverticula, Eustachian tubes, middle ear, sinuses, and the minutest bronchioles; (2) the ventricles of the brain and in the central canal of the spinal cord; (3) the Fallopian tubes (fig. 22) and the mucous membrane of the uterus; (4) the vasa efferentia of the testis and the coni vasculosi.

FIG. 22.—Ciliated epithelium, Fallopian tube. $\frac{1}{6}$″ × 2. C.

The function of cilia is to sweep the surface on which they are found clean, or to aid in the passage of material over them. Thus they clean the respiratory passages, sweeping mucus and entangled dust, etc., towards the mouth. They probably attract the ovum into the Fallopian tubes and sweep it down to the uterus. In the frog's

mouth and œsophagus they help the food along. There is, however, some difficulty in explaining their presence in the

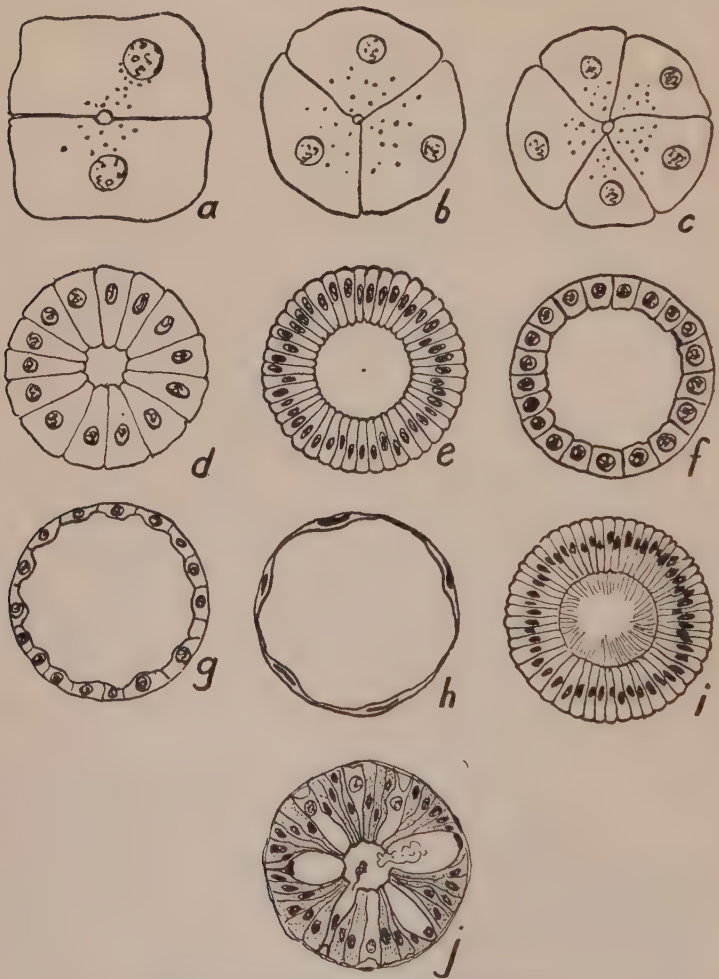


FIG. 23.—Types of glandular epithelium.

*a*. Alveolus consisting of two cells (mammalian liver). *b*. Alveolus consisting of three cells (amphibian liver). *c*. Alveolus of five cells (as often in salivary and pancreatic glands). *d*. and *e*. Alveolus consisting of many cells (e.g. crypts of Lieberkühn and pyloric glands). *f*. Alveolus with cubical epithelium (e.g. thyroid). *g*. Alveolus with subcubical epithelium (e.g. thyroid and inactive mammary gland). *h*. Alveolus with flattened epithelium (e.g. lung). *i*. Alveolus with ciliated epithelium (e.g. epididymis). *j*. Alveolus with columnar and mucous cells—goblet cells (e.g. glands of large intestine).

brain ventricles and the central canal of the spinal cord, and in the œsophagus and stomach of the embryo.

**Secretory** or **Glandular Epithelia**—Invaginations of the epithelia occur in many parts of the body, and we get as a typical appearance epithelial cells (whether pavement, cubical, columnar or ciliated) around a central lumen, or hollow space. Such a group of cells is termed an alveolus. This arrangement is characteristic of most secretory glands, certainly of the glands of external secretion. And so this type of epithelium is called secretory or glandular epithelium. Diagrammatically the appearance of a secretory epithelium is as in fig. 23, *b–d*. The cells are wedge-shaped, and from three or four to a dozen or more cells are grouped round a central space. Into this space the cells secrete, and the material secreted thus passes out to the exterior. There is much variation in (1) the number, (2) the shape, (3) the contents of the cells, and (4) the relative size of the lumen. The alveolus (i.e. the group of cells in question) may have three cells only (see amphibian liver, fig. 23, *b*), or in mammalian liver may be conceived to consist of two only (see fig. 23, *a*) ; in the glands of the plyloric end of the stomach there may be twenty (fig. 23, *e*). Naturally, with the number of cells, the shape varies. The contents of the cells may be granular (mother substances of secretion), and then the granules are arranged near the lumen, except when the cell is fully loaded (see fig. 23, *b, c*). If the granules are mucigen, the cells usually swell and appear glassy (see mucous salivary glands, fig. 102, also figs. 20, 89, 90). In the pancreas there is a definitely staining outer zone (fig. 104). The lumen is almost invisible in a loaded salivary gland, and very small in the liver ; in a mammary or lachrymal gland the lumen is many times the diameter of a cell (fig. 137). These differentia will be more closely dealt with under the different organs in which they occur. See Chapter IV.

## COMPOUND EPITHELIA

These epithelia are found wherever the function of the epithelium is less secretory than protective, and the number of layers varies according to the amount of protection necessary. Thus the vas deferens and the seminal vesicles have two layers of cells, the bladder and ureters three or four layers (fig. 24, also 182 and 183). These last are termed *transitional epithelia*

as showing a transition stage from the single to the many-layered epithelia of mouth, pharynx, etc., called *stratified epithelia*. The cornea (fig. 201), vocal cords, vagina, and os uteri have about six layers of cells, the anal canal and distal part of the urethra a few more, the buccal cavity, pharynx, and œsophagus about twenty (fig. 171), and the skin a great many more (figs. 187, 188).

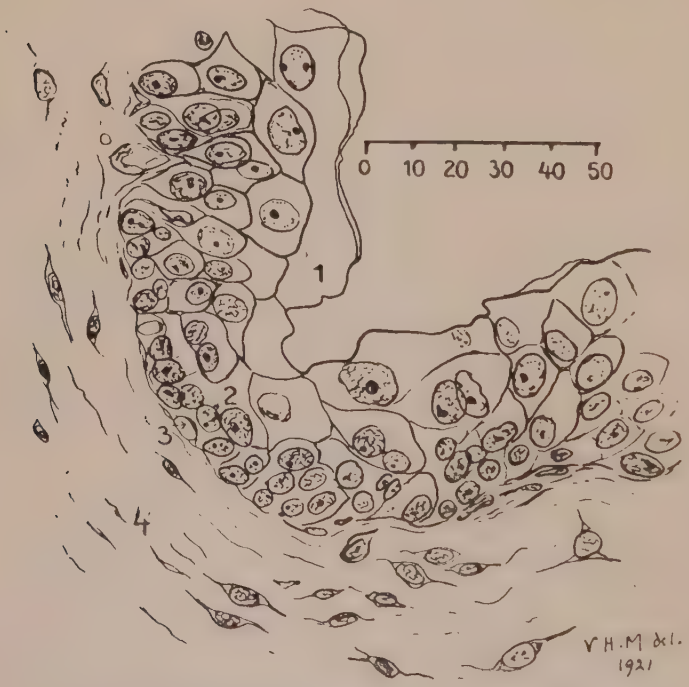


FIG. 24.—Transitional epithelium. Dog's bladder. $\frac{1}{8}$″ × 4. C.
1. Superficial cell of epithelium. 2. Deeper cells. 3. Capillary. 4. Connective tissue.

**Transitional Epithelia**—Taking that of the bladder (fig. 24) as typical, we may say that in the unexpanded condition of the bladder the epithelium is 40 to 50$\mu$ thick. The cells are small in the inner layers and their nuclei are well stained. They are fairly actively dividing (it is said amitotically). As the cells become more superficial they enlarge. Some contain two nuclei. Some are pear-shaped. The most superficial are very large and scale-like, and the

nuclei are but very lightly stained. In fact the cell is becoming effete, and is soon shed and excreted in the urine.

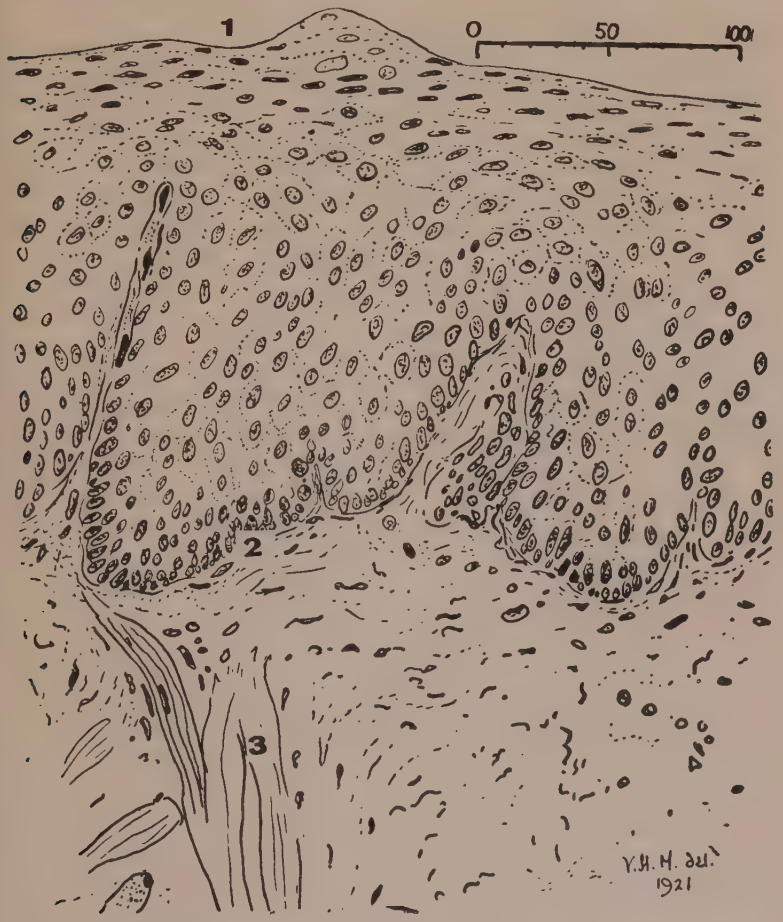


FIG. 25.—Stratified epithelium of tongue. $\frac{1}{6}'' \times 2$. C.

1. Superficial layers of flattened cells. 2. Deepest layers—actively dividing and growing cells. 3. Muscle.

**Stratified Epithelia**—There are two kinds of stratified epithelium, the difference in their appearance depending on their function. Those that line the mouth, pharynx, and œsophagus are not as protective as that covering the skin,

which has to present an impervious and fairly tough surface to the outer world. Or rather, the assaults of nature that the upper alimentary tract has to meet with are not as violent as those on the epithelium covering the skin.

The simpler kind, lining the mouth, pharynx, and œsophagus consists of many layers or strata of cells, the deeper ones being spherical or columnar, their nuclei being easily stained by hæmatoxylin or basic dyes, whereas the outer layers are more flattened and scale-like, and show considerable overlapping, and their nuclei and cell protoplasm stain with much greater difficulty (see fig. 25). The deepest layer of cells is actively dividing, and, under the ordinary high-power mitotic figures, can usually be discerned (see fig. 26). As new cells are formed the other ones become pushed more and more towards the surface. They become pear-shaped, then polygonal and oblate, and finally quite scale-like and flat. The staining power decreases gradually from within out. Whether the cell outlines are visible depends much on the method of fixation. If they are, it is seen that the cells are not closely applied to one another in the deeper layers, nor is the space between them filled (as in pavement epithelium, q.v.) with cement substance. There are channels between them through which probably tissue fluids travel for the nutriment of the cells, and to supply a coagulable fluid, should the outer layers be abraded, to plug the wound and prevent access of bacteria. These channels are crossed by numerous bridges, so that the isolated cell appears surrounded by a mass of prickles (fig. 188).

FIG. 26.—Mitotic figures in stratified epithelium. $\frac{1}{8}$″ × 4. C.

1. Two cells which have just divided. The nucleus of one is being reconstituted, and the chromosomes of the other are in the diaster stage. 2. Diaster and achromatic spindle from another part of the preparation.

In the epithelium covering the skin a similar description applies to the inner layers (about twenty cells deep), but above

and beyond this, i.e. more externally, many further layers are found. The cells, as they push outwards, undergo a chemical change and become unlike those found in the upper alimentary tract. They become more and more horny, and their cell protein consists more and more of cystin (a sulphur containing amino-acid). Before they become horny there is seen a granular layer, a deposit of a fluid material called eleidin being made. This is the *Stratum granulosum* (see fig. 188). As the cells grow older and are pushed nearer the surface, these granules become confluent and lose the power they originally had of being stainable with basic dyes. The cells become glassy or clear (*Stratum lucidum*). Then follows the horny layer composed of many flattened cells, the whole being as thick as all the other layers put together. (In fig. 194, at their deepest the mucous, granular and clear layers measure 250$\mu$, while the horny layer—stratum corneum—measures 300$\mu$, nearly one-third of a millimetre.)

There are special modifications of epithelia, such as hairs, nails, and enamel organs of the teeth, which will be dealt with in a later chapter discussing skin.

## CONNECTIVE TISSUES

The second important class of elementary tissues is the connective tissues. These include areolar, fibrous, and elastic tissues (with some modifications of areolar tissue known as reteform, lymphoid, and adipose), cartilage and bone.

The functions of these tissues are (1) to tie different portions of the body together, and to give its tissues toughness and elasticity: these are the functions of areolar, fibrous, and elastic tissue. (2) To supply light support of a semi-rigid type: for instance, to keep a rather wide lumen, such as that of the windpipe, open, or provide buffers between the bones of a joint, or to supply scaffolding within which rigid bone is built. These are the functions of cartilage. (3) To supply a rigid support to the body of levers upon which muscles can work and alter the disposition of the body. These are the functions of bone.

Connective tissues are distinguishable by their contents. They consist of cells and of ground substance in which the cells exist. The cells may be very different in shape and contents (see figures of areolar tissue, tendon cells, corneal corpuscles, and umbilical cord), according to the tissue in

which they appear, and the ground substance again may vary both according to what it is made of and the specialized elements that are deposited or constructed within it. So when analysing connective tissues, one must always discuss both the cells and the ground substance.

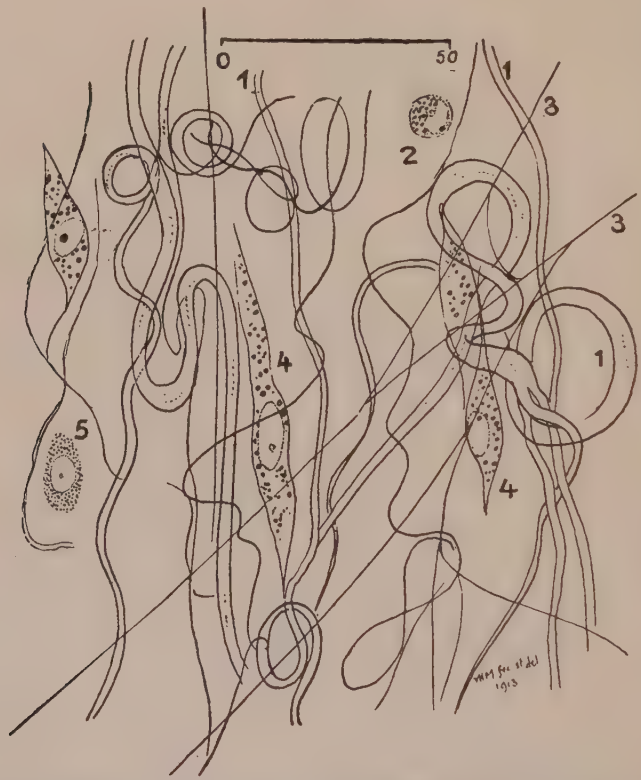


FIG. 27.—Areolar tissue stained intra vitam with brilliant cresyl-blue (rat). 1. Bundle of white fibres. 2. Eosinophil leucocyte. 3. Elastic fibres. 4. Clasmatocyte. 5. Basophil leucocyte, usually abundant in rat connective tissue.

**Areolar Tissue**—Areolar tissue, sometimes called "connective tissue proper," gets its name from its appearance under the microscope: it consists of little areas. It forms the white glistening substance, found immediately under the skin. When a portion of this is spread on a slide and viewed in an isotonic saline solution tinged with a little dye, such as

neutral red or cresyl blue, it will be seen to contain, first, a number of cells, and, second, fibres of two types. The cells are very varied in shape, they may be (1) ovoid cells with granules stained deeply with the dye, (2) round cells, (3) long spindle-shaped cells, or (4) flat, faintly staining cells (fig. 27).

The first two types of cells are migratory, and serve to protect the tissue from bacterial invasion, the third type of cell is probably connected with the formation of fibrils, and the fourth type of cell goes to form a membrane very similar to that of the pavement epithelium.

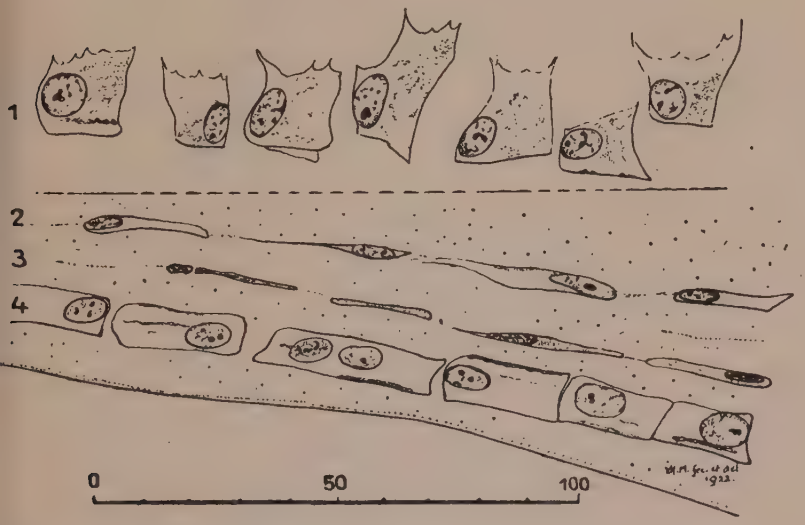


FIG. 28.—Tendon cells. The tendon has been treated with acetic acid to swell the fibres and to make the cells visible. Hæmatoxylin. $\frac{1}{8}'' \times 4$.

1. Cells free from fibres and showing the flanges. 2 and 3. Cells overlaid with fibres, and, in one, little but a flange visible. 4. Usual appearance of cells: the flanges hidden except where vertical. They then appear as lines on the cell.

The fibres are of two sorts: (1) white fibres with a wavy course. There may be many fibres or few in a bundle, and they lie parallel side by side. If a bundle splits, as it often does, the individual fibres do not split, and there is no anastomosis between the fibres. They have the characteristic of swelling with acetic acid, and can easily be distinguished by this means. (2) faintly yellow fibres (fewer in number). These are the elastic fibres. They pursue a straight course across

the field, and apparently anastomose with one another. If broken across, they coil up and show their elastic nature.

White fibrous tissue is found in especial development in the tendons to the exclusion of nearly everything else: the fibres run straight and parallel in the direction of the tendon. In between them, and arranged in rows, are the tendon cells. By swelling the fibres with acetic acid the cells can be made visible, and then usually appear as rectangles containing an oval nucleus and faintly granular protoplasm (fig. 28). Such

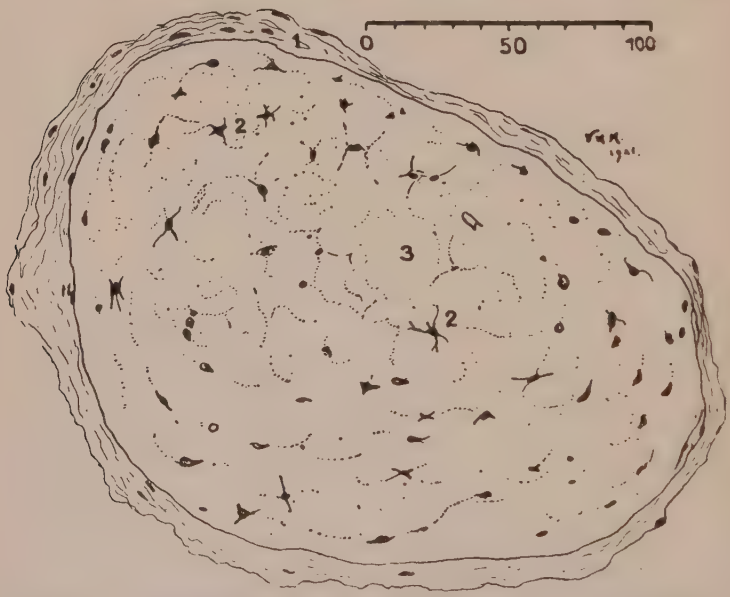


FIG. 29.—Transverse section of small tendon. $\frac{1}{8}$" × 2. G.A.H.
1. Connective tissue sheath. 2. Stellate tendon cells. 3. Fibres cut transversely.

a cell, when focused carefully, will show lines upon its surface parallel with the greater length of the cell. The explanation of these lines is that cells send up thin phlanges between the fibres, so that if you can separate cells completely from their fibres you can get such an appearance as in the upper part of fig. 28. The straight line on the rectangular cell is the phlange seen from above, in cross-section the cells of the tendon appear star-shaped, the phlanges forming the rays of the star (fig. 29).

Covering the tendon and permeating between these bundles will be found ordinary areolar tissue. The outside layer of this consists of pavement epithelium (see fig. 14).

**Yellow Elastic Tissue**—In some places in the body, for instance the ligaments between the vertebræ, the ligaments and cartilages of the larynx, and in the arteries, and to a lesser

FIG. 30.—Tendon. The tendon has been teased and stained with acid fuchsin, which stains white fibrous tissue. C.

extent in the veins, elastic tissue is gathered together into a ligament or membrane in which it is the predominant feature—see, for example, fig. 31, which represents a transverse section of the ligamentum nuchæ of the ox. The clear shining masses, are elastic fibres seen in transverse section, and the substance between them is areolar tissue. As in the tendon the fibres are tied together by ordinary connective tissue. The distinctions between these two classes of fibrous tissue are: (1) the disposition of the fibres, whether wavy or straight;

(2) their reaction to acetic acid; (3) their staining properties with dyes. White fibrous tissue stains deeply with acid fuchsin, yellow elastic tissue with picric acid. So that a section stained with van Gieson's stain, which contains these two dyes, readily shows which fibres are white fibrous tissue and which yellow elastic tissue.

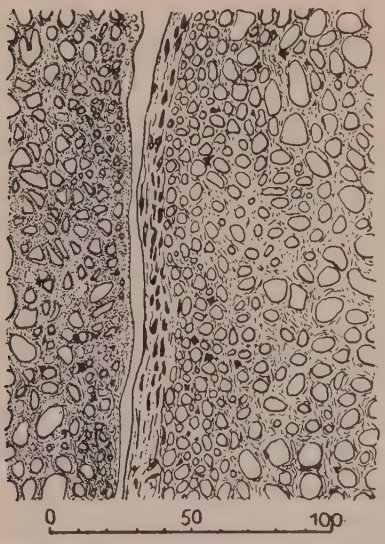


FIG. 31.—Transverse section of a ligament containing many elastic fibres. $\frac{1}{6}'' \times 2$. C. (Ligamentum nuchæ. Ox.)

The elastic fibres show as white polygonal spaces in a grey background representing white fibrous connective tissue. The nuclei of the connective tissue cells appear as small stellate masses except where the fibres are running longitudinally, e.g. around one of the divisions of the ligament.

## SPECIAL DEVELOPMENTS OF AREOLAR TISSUE

**Reteform and Lymphoid Tissue**—In such organs as lymph glands, or in the glands of the intestine, or in the marrow, we find a type of connective tissue which is really a modification of areolar tissue. In the lymph glands, for instance, the white fibres of the trabeculæ are continuous with a very fine network of fibres that goes throughout the medulla of the gland (fig. 32). Similar structures are found in the marrow and all glands. The fibres that compose this network have the same chemical characteristics as those of the white fibres, so that there is really no need to separate this form of tissue off from areolar tissue. In the meshes of the network there is no mucoid substance as in areolar tissue, but its place is taken by fluid, the ground substance having practically disappeared. The cells of lymphoid and reteform tissue are wrapped round these fibres, with the result that you have the appearance of a network (reticulum) composed of cells rather than fibres. Such an appearance is observed in the diagrams illustrating, e.g., the cardiac end of the stomach (fig. 96), the villi of the small intestine (fig. 176), etc. The

function of the lymphoid (or reteform) tissue is to support and conduct the blood vessels throughout the glands, to form a basement membrane for the glandular epithelium, and to retain the cellular elements of the tissue in their place.

**Adipose Tissue**—Adipose tissue is a tissue in which cells containing large amounts of fat are predominant. It has a wide distribution. It is found: (1) under the skin in large amounts—invariably it is found in the palms of the hands and the soles of the feet, (2) around internal organs such as

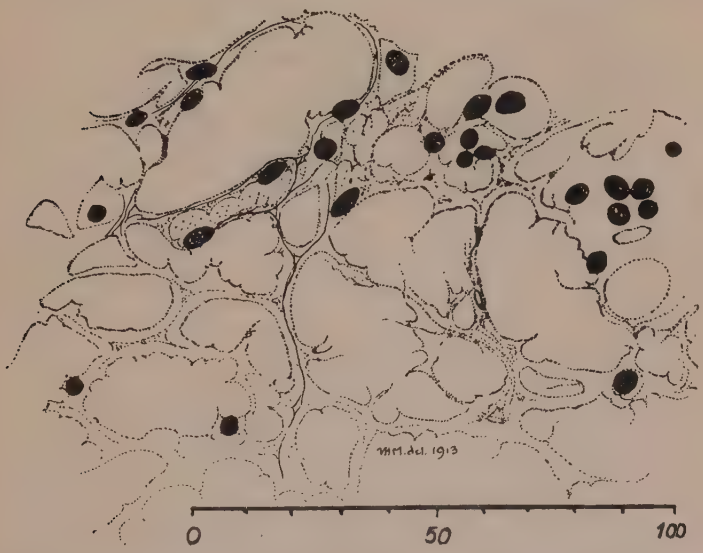


FIG. 32.—Reteform connective tissue from a washed lymph gland. $\frac{1}{6}'' \times 4$. L.

the kidney, (3) in the mesentery and omentum, (4) along the courses of the blood vessels and nerves, e.g. behind the eyes, and (5) in the marrow. There are some few places in the body from which it is always absent, e.g. the cranial cavity, the eyelids, and the penis. When found, it is always accompanied by a large number of blood capillaries and in close relation, too, to the lymph channels.

The structure of adipose tissue is essentially that of a groundwork of areolar tissue in which there are large ovoid cells (often in large groups) some 40–100$\mu$ in diameter. Where there are many cells together, they take on the hexagonal

form of cells in plant tissues, e.g. pith, owing to the pressure. The cell is loaded with fat, contains almost no protoplasm, and the nucleus is pressed flat. In ordinary preparations

FIG. 33.—Adipose tissue from the sheath of a nerve fixed in osmic acid. C.

1. Fat cells with the fat stained and made insoluble in xylol by osmic acid. 2. Fat cells into which the osmic acid has not penetrated, so that the fat has washed out in mounting. 3. Perineurium. 4. Nerve fibres.

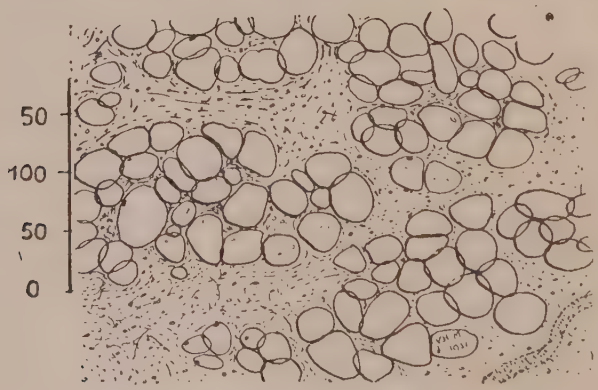


FIG. 34.—Adipose tissue from the mesentery.

The ovoid white spaces represent cells from which the fat has been washed by xylol. The back ground is ordinary areolar tissue.

the appearance of adipose tissues varies with the treatment that the tissue has received. When the tissue is fixed and mounted in fluids that do not dissolve fat, the cell appears highly refractive owing to the fat present. When cleared with

xylol the fat is completely dissolved out of the cell, with the result that nothing but a network of cell membrane and protoplasm is left. If the tissue has been fixed with osmic acid, osmuim is precipitated in the fatty substance, and makes it insoluble. Consequently under the microscope we see heavy black masses. Fig. 33 illustrates this very well.

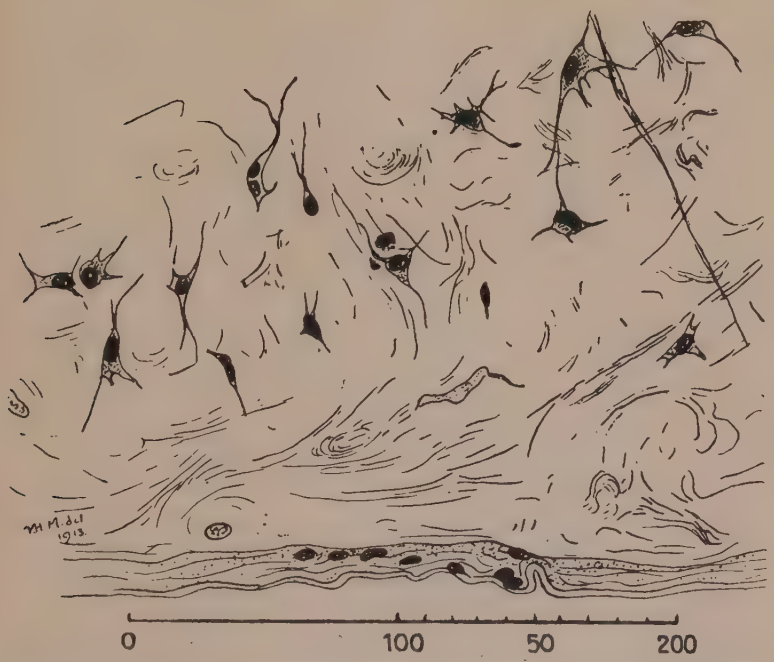


FIG. 35.—Embryonic connective tissue corpuscles. Wharton's jelly from umbilical cord.

It is from an osmic acid preparation of a nerve with its sheath of connective tissue, in which is found a small amount of adipose tissue. The osmic acid has not penetrated the whole way into the fat: consequently we see a jet-black portion into which it has penetrated and another portion from which the fat has been washed by xylol, leaving a network of cell membrane and cell protoplasm. As a comparison with this a drawing of a mesentery, which has been fixed in alcohol and cleared with xylol, is given (fig. 34). Here the fat cells

appear as void empty spaces, with here and there a compressed nucleus visible.

The function of adipose tissue is mainly that of the storage of surplus combustible material. Secondarily, it forms cushions for important organs, such as nerves, blood vessels, and kidney.

Another type of connective tissue, with which the student may meet, is that of the embryonic connective tissue found in

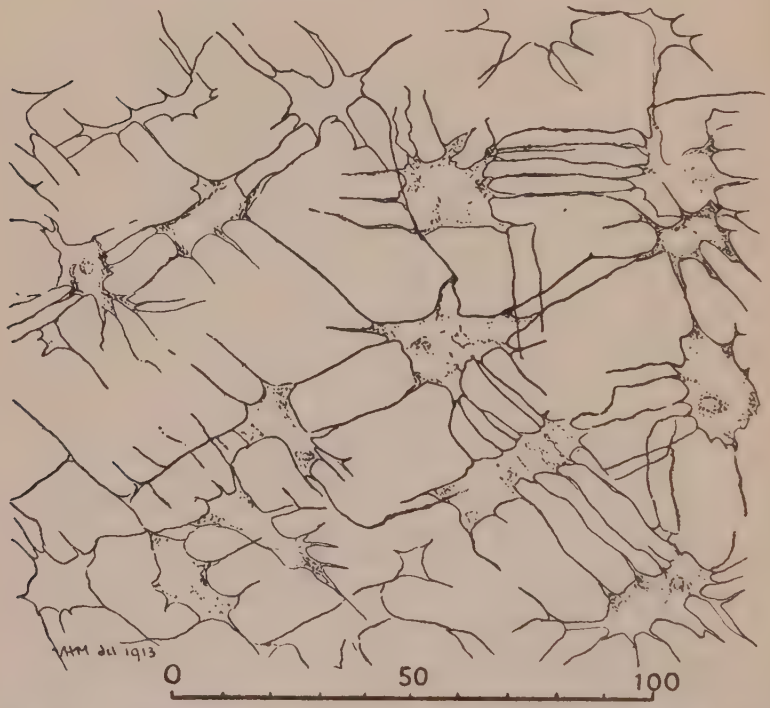


FIG. 36.—Connective tissue corpuscles of the cornea, stained with gold chloride and seen from above. $\frac{1}{8}'' \times 4$. L.

the umbilical cord. Here the jelly-like ground substance is the most obvious element—whence it is named after its discoverer, Wharton's jelly—in which are found branched connective tissue corpuscles of an embryonic type, together with a small amount of white fibrous tissue running in all directions (see fig. 35).

Fig. 36 shows the arrangement of the connective tissue cells

of the cornea of the eye, where a much more regular arrangement of cells and fibres is necessary.

## CARTILAGE

This substance is familiarly known as gristle, and is bluish white or yellow, according to its composition. It is markedly elastic and light, and possesses strength without rigidity. Cartilage may be divided into two types: (*a*) temporary, which forms the scaffolding in which bones are laid down, and disappears in adult life, and (*b*) permanent, which persists

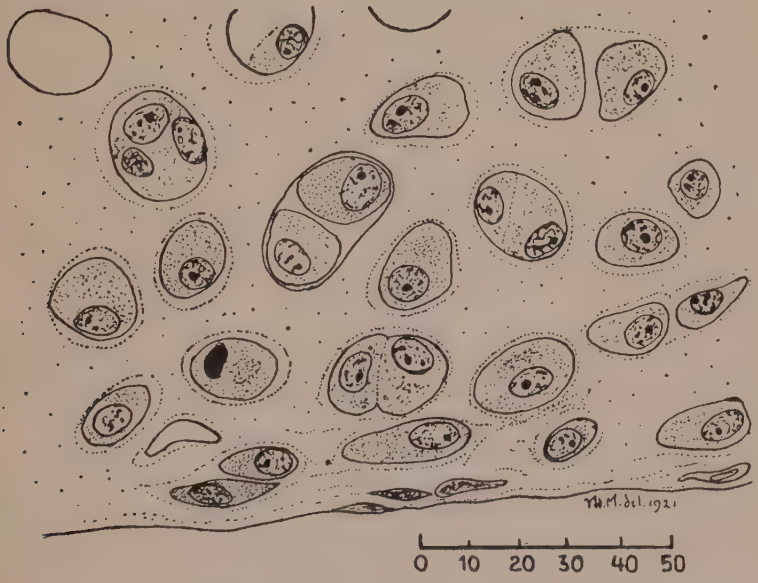


FIG. 37.—Hyaline cartilage. $\frac{1}{8}'' \times 4$. C.

in adult life. Permanent cartilages are found in the articular cartilages at the ends of bones, in the interarticular cartilages (both of which have the function of absorbing shocks, acting as cushions); in the costal cartilages, which form an important part of the skeleton of the thorax; in those of the external ear, Eustachian tube, nose, larynx, windpipe, bronchi, and bronchioles. The function of these last-named cartilages is to maintain the shape of the organs of which they form part.

The histological classification of the permanent cartilages

is made according to : (1) the ground substance, and (2) the presence or absence of fibres in that ground substance. When the ground is clear the cartilage is termed hyaline. In hyaline cartilage (see fig. 37) we find ovoid cells embedded in a translucent ground substance. The cells, which are approximately 20$\mu$ long, contain one nucleus with one or more nucleoli and a distinct chromatin network. The protoplasm of the cells is faintly granular, and when the cell is old there may be a few globules of fat. Though sometimes the cells are single, they are more usually grouped in twos, fours, or eights, according to the number of times the cell has divided. Marked in the matrix there is usually a line surrounding the group, more heavily stained with basic stains than the rest of the matrix. This is called the capsule, and is of importance in understanding the structure of the other types of cartilage. Each cell has its own capsule round it. When it is one of a pair there is in addition a capsule round the pair, and when this pair forms a part of a group of four there is a still further capsule round the four, and so on. Cartilage under the microscope has such a characteristic appearance that once it has been seen and understood it should always be easily recognized.

The distinction between the various types of hyaline cartilage has to do more with the arrangement of the cells and cell groups, and the amount of deposit in the ground substance than with anything else.

**Articular Cartilage**—The first variation is to be found in the articular cartilages where the groups are flattened at, and near to the surface, and lie parallel with it. And at the edge the cartilage cells take on the appearance of branched connective tissue cells, into which connective tissue cartilage almost insensibly merges.

**Costal Cartilage**—In this cartilage the cells near the surface are flattened and arranged parallel to the surface ; the deeper cells (fig. 38) are in groups of rather large numbers ; deeper still, the cells show considerable deposition of fat, and there usually is at this depth a granulation of the matrix due to the deposition of calcium salts. Very frequently the central portion of costal cartilage is ossified (see ossification of bone).

**Fibro-Cartilage**—In white fibro-cartilage the matrix is permeated with wavy white fibres, such as characterize a

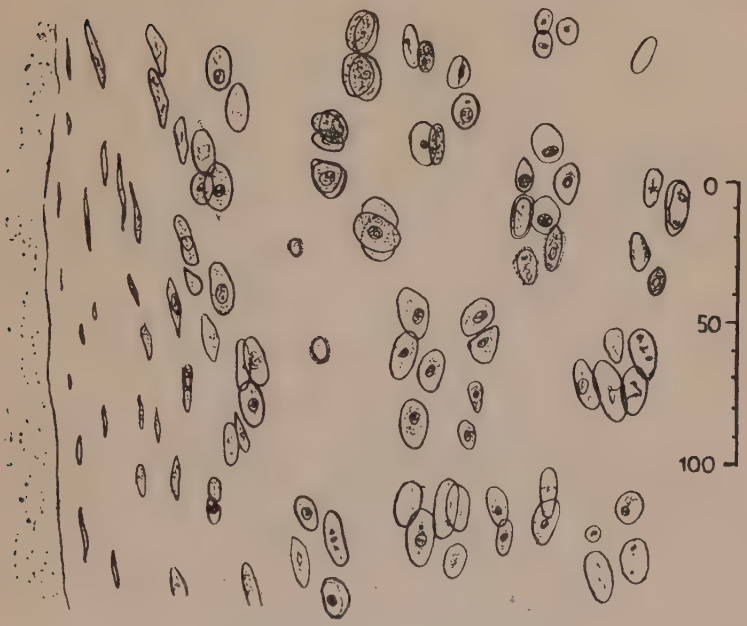


FIG. 38.—Costal cartilage. $\frac{1}{6}$" × 2. C.

The cells near the border of the rib are flattened. Deeper they are oval, arranged in large groups, the protoplasm is vacuolated and often contains fat.

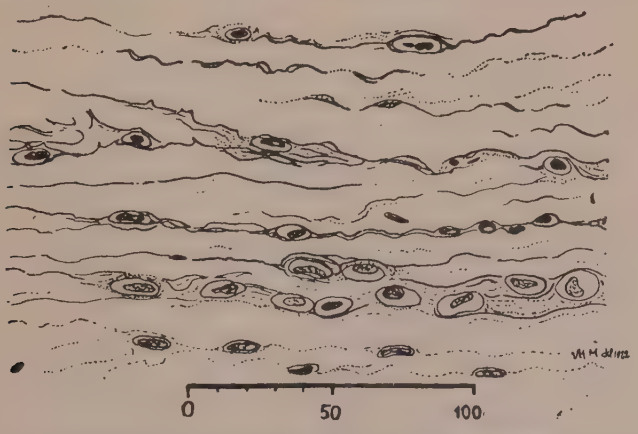


FIG. 39.—Fibro-cartilage (semilunar cartilage of knee-joint). $\frac{1}{6}$" × 2. C.

The fibres are arranged in parallel lines, with the cartilage cells in rows in between. Compare with tendon cells, Fig. 28.

tendon. Near the surface the fibres are parallel with each other, and the cells follow their general direction, with the result that white fibro-cartilage closely simulates the appearance of a tendon (cp. fig. 39 with fig. 28). More deeply the fibres run in all directions, are fewer in amount, and the cells are scattered (fig. 40). The distinguishing mark of white fibro-cartilage is the typical appearance of the void cartilage cell surrounded by its capsule, into which no fibres penetrate. Examples of fibro-cartilage are found in the inter-articular

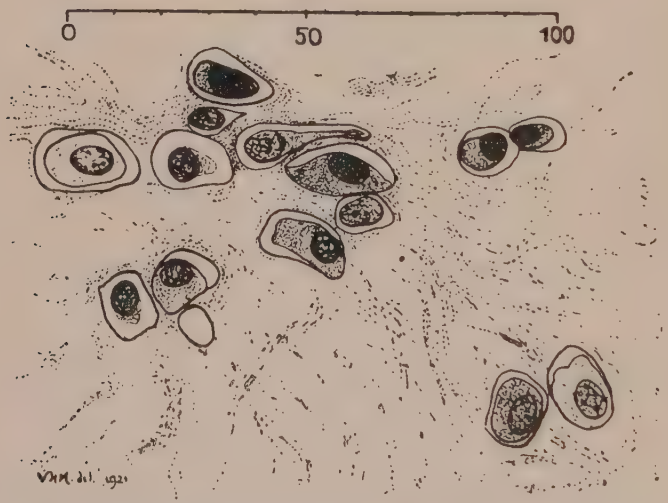


FIG. 40.—Fibro-cartilage (intervertebral disc, near the centre). $\frac{1}{8}$" × 4. C. The fibres are not so distinct nor so regularly arranged as those near the surface.

discs (e.g. vertebral and semilunar cartilages) and in symphysial cartilages.

**Yellow** or **Elastic Fibro-Cartilage**—In this type of cartilage the matrix is permeated with elastic fibres running in all directions, but again never penetrating the capsule. This cartilage is best distinguished by staining specially for elastic fibres, although staining with van Gieson's stain will serve to distinguish white from yellow fibro-cartilage (figs. 41 and 42). White fibres take up the acid fuchsin of the mixed stain, the yellow fibres the picric acid. Elastic fibro-cartilage is found in the pinna of the external ear (fig. 43),

the Eustachian tube, the epiglottis, and the arytenoid cartilages.

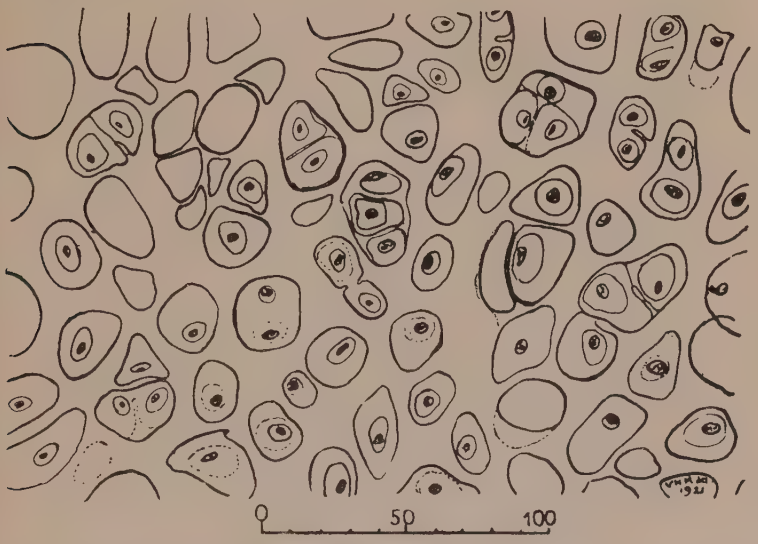


FIG. 41.—Elastic cartilage. $\frac{1}{8}$" × 2. C.

This drawing is from a preparation stained to show cells, but not the nature of the matrix. It therefore closely resembles the one of hyaline cartilage, Fig. 37.

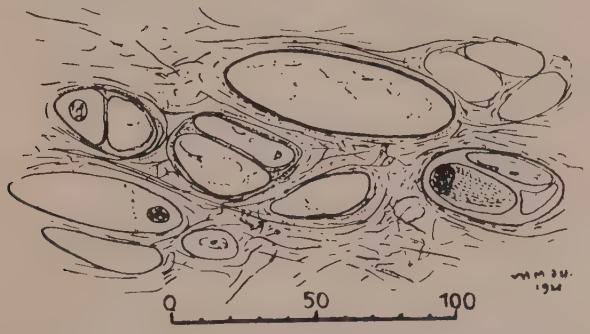


FIG. 42.—Elastic cartilage, stained for elastic fibres. $\frac{1}{8}$" × 2. C.

Compare with Fig. 41, in which the elastic fibres are not shown. The elastic fibres do not enter the capsule of the cells.

Covering all the cartilages, except those of the joints, is found a membrane, composed of white fibrous tissue and

containing blood vessels, which is called the perichondrium. Similar connective tissue membranes are to be found over almost all important organs, and, except when given the name of their discoverer (e.g. Glisson's capsule) or some fantastic name like *pia mater*, are called by names that indicate their position (e.g. periosteum = around the bone, perineurium = around the nerve, perimysium = around the muscle).

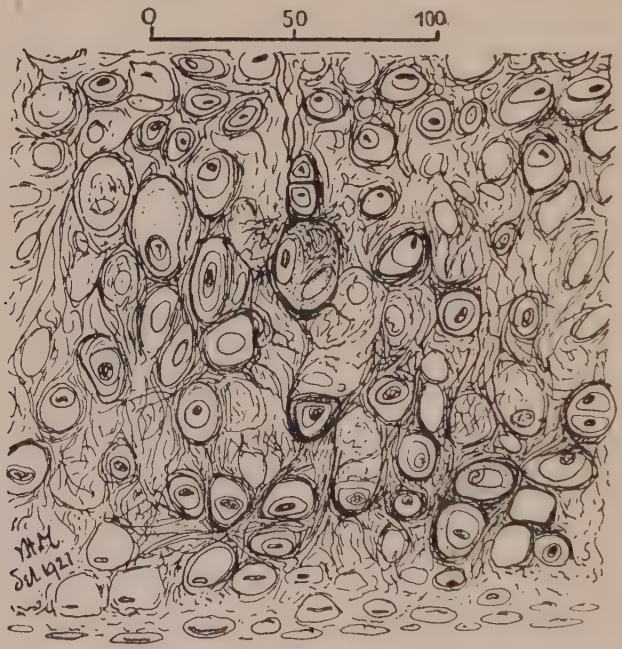


FIG. 43.—Elastic cartilage (ear). Stained for cells and elastic fibres. $\frac{1}{6}$" × 2. E.C.M.

Compare with Figs. 41 and 42.

## BONE

The bones are the strongest and rigidest tissues of the body, with perhaps the exception of the teeth. Their strength is obtained by the deposition in a connective tissue of insoluble salts of calcium, mainly phosphate and carbonate. Sixty-six per cent. of bone is composed of mineral matter. When these salts are dissolved out by dilute mineral acid the tissue remaining behind is softer and more flexible than cartilage,

and on boiling yields gelatine in large quantities. In this it resembles areolar and fibrous tissue rather than cartilage.

There are two methods of treating bone for histological purposes: (1) by decalcification of the bone by steeping in dilute acid, and when the mineral salts are completely dissolved out, treating the resultant substance much as an ordinary histological tissue; (2) by grinding down thin slips of the

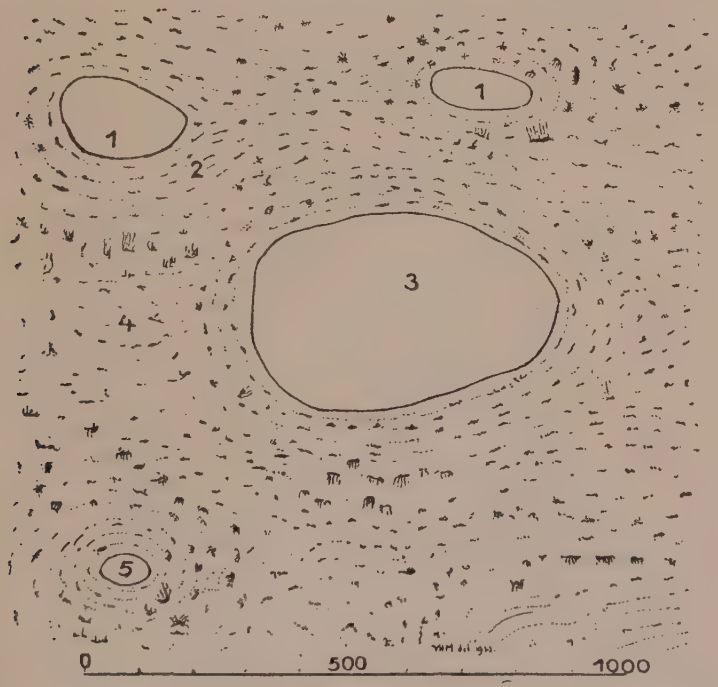


FIG. 44.—Bone. Drawing made from a section ground thin and mounted dry. $\frac{3}{8}'' \times 1$. P.C.E.

1, 1. Two Haversian canals cut somewhat obliquely, the one passing into the other either above or below the level of the section. 2. Haversian lamellæ. 3. Large Haversian system. 4. Interhaversian lamellæ—the corpuscles are irregularly placed. 5. Small Haversian system.

bone till they are so thin as to be transparent. Naturally the second method is the more tedious and costly, and the average student will rarely be provided with such except as demonstration specimens.

Ordinary means of analysis of a bone with a hand lens and saw will show that over the whole bone, except at the joints,

there is a membrane, the periosteum. (This consists of connective tissue. Outside there is a preponderance of white fibres, deeper there are many elastic fibres. In the meshes of this periosteum are to be found a rich supply of blood vessels and nerves, which ramify there and then send their branches into the bone substance. Adjacent to the bone proper is a layer of cells of great importance in building the bone or repairing it when damaged.)

FIG. 45.—Bone. Small Haversian system from the same section as 44. $\frac{1}{4}$" × 1. P.C.E.

1. Bone corpuscle with canaliculi. 2. Canaliculi extending beyond the limits of one lamella into the next. 3. Haversian canal surrounded by concentric layers of bone (lamellæ) and bone corpuscles.

Next, by this means, bone will be seen to consist of two types: compact and spongy (or cancellous). These pass, on minute analysis, insensibly into one another, but to the naked eye the division is clear and useful enough. The bones of the skull have external and internal layers of compact bone with spongy bone in between. The heads of long bones

such as the femur consist of a thin external layer of compact bone with spongy bone inside. The shafts have a much thicker layer of compact bone outside, which increases in thickness towards the middle of the shaft, and there is less of the spongy bone.

Under the microscope all bone, whether compact or spongy, is shown to be full of holes. Those in the compact bone are minute and, after their discoverer, are called Haversian canals. The average width of these is 50$\mu$, the narrower being met with at the circumference of the bone, the wider nearer the inside. The Haversian canals are short and open into one another obliquely. Externally they communicate with the surface, and internally with the hollow spaces of the spongy tissue or with the medullary [1] spaces (figs. 44, 45).

These canals carry blood vessels, lymph vessels, and nerves throughout the bone and into the medullary spaces. The blood vessels are derived from those in the periosteal sheaths. Each Haversian canal is surrounded by concentric layers of bone, termed lamellæ, and, in addition, there are seen lamellæ parallel to the surface of the bone, and others, more irregular, in between the Haversian systems. The reason for this will become more obvious when the ossification of temporary cartilage is studied.

In the ordinary preparations of decalcified bone there will be seen, here and there, and arranged in concentric rings around the canals and in between the lamellæ, cells called bone corpuscles (fig. 46). These are more obvious, or rather the spaces they occupy between the lamellæ become more obvious, in a ground section of bone. The bone dust formed by grinding fills the spaces, the *lacunæ*, in which the cells live, and makes them appear opaque in section. The same happens to minute channels through which the fine protoplasmic threads of the cells pass, making communication with the neighbouring corpuscles, and these show up as spidery lines uniting the various black lacunæ. Between the Haversian systems the lacunae are more irregular.

Clearly the cells, which are homologous with the lamellar cells of connective tissue, are responsible for the upkeep of the bone substance, and the canaliculi put them into intimate touch with the bone substance and each other.

The cancellous (spongy) tissue, and the hollow shaft of

[1] Medulla = marrow.

long bones, contain marrow, the description of which must be left till later. It consists of adipose tissue, of a connective

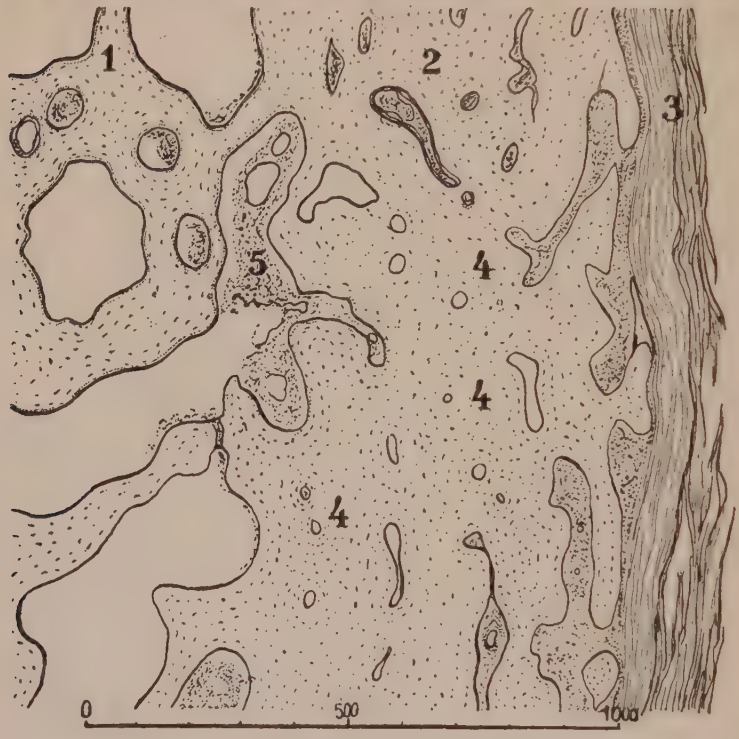


FIG. 46.—Decalcified bone. $\frac{3}{4}$" × 1. G.A.H.

1. Cancellous or spongy bone. 2. Compact bone. 3. Periosteum. 4. Haversian systems. 5. Marrow.

tissue of the reteform type, in the *meshes* of which are masses of free cells comparable with those of the blood, the lymph glands and the migratory cells found in connective tissues.

## FORMATION OF BONE

**1. By Ossification in Cartilage**—This process is one of the most amazing that occurs in the animal body. Nearly every bone of the body is originally laid down in cartilage, the only exceptions being the bones of the cranial vault and the majority of the bones of the face.

By the time that adult life is reached every vestige of

cartilage has been swept away and bone put in its place. This occurrence may take place even more rapidly in the antlers of the deer, which are renewed every year. The growing point is cartilage and is rapidly transformed into

FIG. 47.—Ossifying cartilage (fœtal animal). $\frac{3}{8}$" × 2. C.

The older cartilage is to be found in the middle of the preparation, and the newly formed towards each end. For reference letters, see text. Compare Fig. 48 and diagram, Fig. 49.

bone, so that yearly transformation of cartilage into bone is completed in the time between February, when the antlers are shed, and the mating season.

In fœtal life ossification has already begun. The first

rough sketch of the bone is formed in cartilage. The cartilage elongates by growth towards each end. Consequently the older cartilage cells are in the centre, and it is in the centre of such a mass of cartilage that ossification begins. This consists of an irruption of cells developed from the inner layer of the periosteum, followed by blood vessels and nerves, the cells eating up and completely destroying the older cartilage and laying down true bone round the blood vessels (fig. 47). Consequently, if we take such an ossifying bone and move from the position of the recently developed cartilage cells towards the ossification, we shall pass through a series of more and more mature cartilage cells, even, it may be said, more and more effete cartilage cells, to the area in which they are destroyed.

(1) We see ordinary hyaline cartilage, the description of which tallies almost exactly with that of the hyaline cartilage elsewhere [1]: the cells are ovoid, they have well-stained nuclei, the protoplasm is granular, but contains no fat, the matrix is also clear and shows no granulations (fig. 47, *a*).

(2) Next we find that the cells are now arranged in vertical columns, running parallel to the direction of the shaft. The tendency to grouping of the cells is still obvious, those at the end of each short column being more pointed and smaller than those nearer the middle. The protoplasm of the individual cells appears vacuolated and contains fat (fig. 47, *b*).

(3) We now come to cells still preserving the columnar arrangement, but showing considerable degeneration of their contents. The nuclei no longer stain well, and the protoplasm is ragged and vacuolated, and contains considerable fat. The matrix is still clear (fig. 47, *c*).

(4) We now meet cells considerably larger, the cell contents are very much degenerated, and the matrix contains a heavy deposit of calcium salts (fig. 47, *d*).

(5) We meet the area of invasion.

Cells under the perichondrium, or, as it should now be called, the periosteum, actively proliferate and invade the cartilage in direction at right angles to the length of the bone and to the columns of cartilage cells [2] (fig. 47, *e*). The invading cells are of two types: first, large multinucleate cells, 30 or 40$\mu$ in

[1] Fig. 37 gives a high-power view of such an area.

[2] In normal ossification this edge is very straight, almost as if drawn with a ruler. If it be ragged the ossification is abnormal, pointing to rickets, scurvy, etc.

diameter, whose function is to destroy the cartilage matrix. These cells are called osteoclasts (fig. 48). Logically at this stage they should be called chondrioclasts, or cartilage destroyers. The other type of cell is much smaller, and possesses one well-staining nucleus only, and its function is that of bone-building. It is, therefore, called an osteoblast.

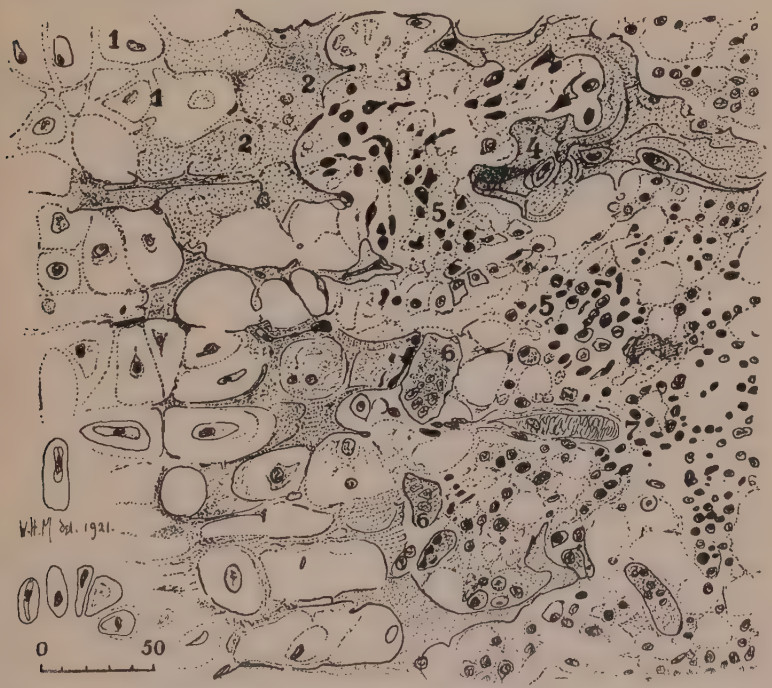


FIG. 48.—Ossifying cartilage at the line of ossification. High-power ($\frac{1}{6}$″ × 2) view of the same cartilage as in Fig. 47.

1. Degenerated cartilage cells. 2. Matrix of cartilage with deposit of calcium salts. 3. Line of invasion of cartilage by chondrioclasts (osteoclasts) and osteoblasts. 4. Newly formed endochondral bone. 5. Groups of osteoblasts. 6. Osteoclast. 7. Capillary containing blood corpuscles.

Before any active destruction of cartilage has taken place, a thin strip of true bone has been formed externally by the osteoblasts close to the periosteum. This is known as periosteal bone (figs. 47 and 49). The osteoclasts then invade the effete cartilage and proceed upwards between the columns of matrix, and break down the thin horizontal division between the cartilage cells. Often one can see an osteoclast applied

to a vertical column of matrix, eating it away (fig. 48). The osteoblasts then settle around the blood vessels that have

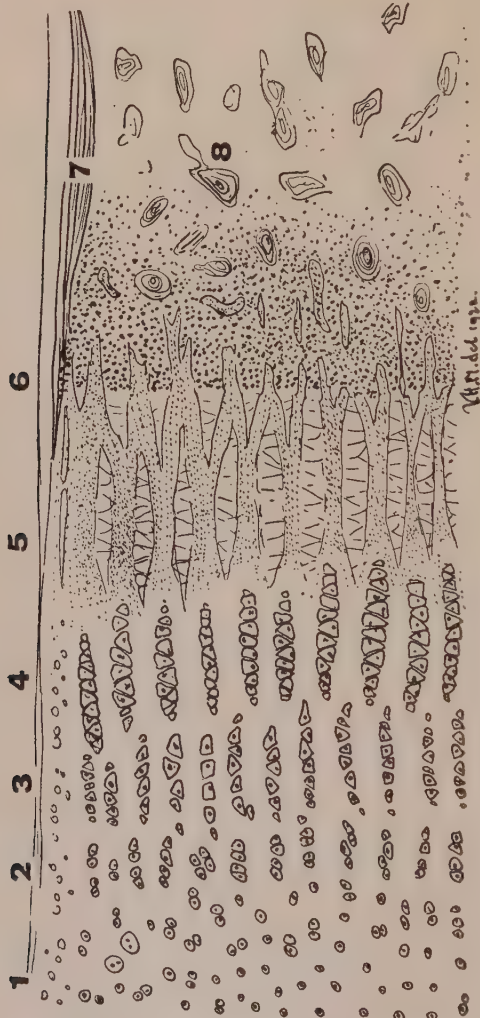


FIG. 49.—Diagram of ossifying cartilage.

1. Newly formed hyaline cartilage. 2. Older cartilage cells. 3. Cartilage cells arranged in rows. 4. Cartilage cells beginning to degenerate. 5. Degenerated cells. Calcium salts deposited in the matrix around them. 6. Line of advancing invasion by osteoblasts and osteoclasts. 7. Periosteal bone. 8. Endochondral bone.

entered with the invading host and start to form true Haversian systems round them. First one lamella is formed, and then a second and a third, until finally the whole space originally

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filled with cartilage has been turned into a compact mass of Haversian systems. This bone is called endochondral bone. As in front of the invading host the cartilage degenerates, still further destruction of the cartilage takes place with the still further deposition of bone. Thus the formation of bone proceeds in two opposite directions, from the centre of the shaft out towards the extremities. Usually the osteoblasts are not content with the first structure that they build, but osteoclasts destroy it and osteoblasts replace it by a second or even a third and more regular arrangement. Osteoblasts which are caught into the bony structure that they build settle down there and become the bone corpuscles of mature bone.

Along with the invading cells, or possibly derived from them, come cells which form the marrow of the bones.

The description given above applies to the shaft of a long bone. The distal and proximal ends of the long bones have their own centres of ossification, and in the terminal phalanges ossification takes place from the tip towards the base. Sometimes the whole of the cartilage is swept away before any but periosteal bone is formed. (For the centres of ossification in bones and for variations of the process the student is referred to textbooks of anatomy.)

It is clear from the relative shapes of the fœtal and adult bones that not only is bone-building going on till adult life is reached, but that a continual destruction and reconstruction is taking place, so that at, say, the head of the femur there is a removal of bone substance on the lower aspect of the head taking place, as well as deposition of bone at the upper (fig. 50).

**2. Ossification in a Membrane**—Some bones, notably those of the roof of the skull, are laid down in connective tissue and not in cartilage. The tissue is vascular and the cells are of an embryonic type (i.e. somewhat like those of Wharton's jelly). There is considerable fibrillation and the fibres are the white fibres of connective tissue. If we take such a tissue as it is beginning to ossify, we find, in addition to the connective tissue corpuscles, numbers of larger cells, with well-staining nucleus and protoplasm. These preside over the formation of the bone. These are, of course, the osteoblasts. In the region of the osteoblasts we see: (1) a deposition of calcium salts occurring between the fibres, and (2) an extension and increase of the fibres, which, though continuous with those of the connective tissue, appear stiffer

and straighter. Apparently the fibres are not ossified themselves, but the substance between them is. The advancing edge of ossification is preceded then by a fringe of osteogenic fibres, and the osteoblasts follow and aid in the deposition of the dense mass of calcium salts. Osteoblasts which get embedded in the mass of bony spicules form the lacunæ in the bone substance, and themselves are termed bone corpuscles.

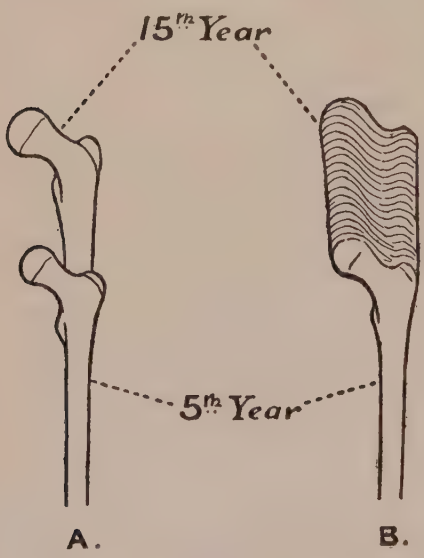



FIG. 50.—From Keith's "Engines of the Human Body."

*A*. The upper end of the thigh-bone at the fifth year, above which is indicated the position which the head and neck will occupy when the fifteenth year is reached. *B*. The form the thigh-bone would assume by the fifteenth year if there were not continual remodelling of the bone by the osteoclasts and osteoblasts. (Reproduced by kind permission of Messrs. Williams & Norgate.)

The vascular network of the tissue determines the course of the ossification, for ossification takes place in the centre of the meshes at a place farthest from the blood vessels. The spicules, osteological fibres, in the advancing ossification, bend away from the blood vessels, and thus form arches round them, enclosing them in a bony tunnel. The final result of ossification is a bony spongework, the short intercommunicating canals of which contain blood vessels, and a layer of osteoblasts. The lamellæ of the bone are concentric with these canals except immediately under the periosteum, where they are parallel with the surface. In spite of the difference of the mode of origin of membranous bone, the final result is very like that of cartilaginous bone and distinguishable by experts only.

## MUSCULAR TISSUE

Muscle is that tissue which brings about: (1) movements of the skeleton of the body, and so enables it to alter its place or the disposition of its parts in space, or (2) the movements

of the internal organs, altering their size and shape, particularly the size of the lumen of hollow organs.

Histologically muscle can be divided into: (1) striped muscle, (2) unstriped or smooth muscle, according to whether the muscle cells show a cross-striation or not. Striped muscle is further divided into: (*a*) skeletal muscle, in which the component cells are long and unbranched, and (*b*) cardiac muscle, in which the cells are short, and by means of short branches communicate with each other.

Striped muscle is found where movement of the tissue is rapid. Skeletal striped muscle is found in (*a*) the muscles that move the skeleton, (*b*) the tongue, (*c*) the upper part of the œsophagus, and, in birds where rapidity of focusing the eye is essential during a swoop downwards, etc., in Crampton's muscle. Cardiac muscle is found in the heart only. Unstriped muscle is found forming an important part of the walls of the alimentary canal from the œsophagus to the anus, of the veins and arteries, of the bladder, uterus and uro-genital organs generally. It enters into the formation of the capsule and trabeculæ of the spleen, of the prostate gland, into the iris and ciliary muscles of the eye, it erects the hairs of the body and produces "goose flesh," causes the crinkling of the skin of the scrotum, and enters into the structure of the sweat glands.

**Skeletal Muscle**—In the skeletal muscles there is a very great variation in size and shape. A single muscle may be composed of a few fibres (as the stapedius and tensor tympani), or it may contain many thousands (as the quadriceps extensor of the thigh). Muscles are usually considerably longer than broad, and at one end they take origin from a bone, whilst at the other end they are inserted into a tendon. In the abdominal muscles the muscle substance is interrupted by tendon, and it has been suggested that in the same way intercostal muscles are interrupted by the ribs. In transverse section the arrangement of the muscle is seen to be similar to that of a tendon, or, as we shall see later, to that of a nerve trunk. Over the whole is a well-marked connective tissue sheath called the epimysium. This sheath may contain some fat cells and blood vessels. Branches of this *epimysium* run in between the fibres of the muscle and divide them up into bundles called fasciculi. This structure is called the *perimysium*, and is useful not only as connective tissue, but as a

means of conduction of nerves and blood vessels to the fibres. The fasciculi are bundles of muscle fibres proper, which are separated from each other by a further ingrowth of connective tissue from the perimysium called the *endomysium*. In the endomysium the capillaries, so important to muscle contraction, run.

Looking at the individual muscle fibres, we see that they vary greatly in diameter, though in any one muscle they are approximately the same. The maximum diameter may be as much as 100$\mu$ and the minimum as little as 10$\mu$. Those shown in figs. 51 and 52 run approximately 20–30$\mu$. The length of individual fibres is remarkably great, and may be

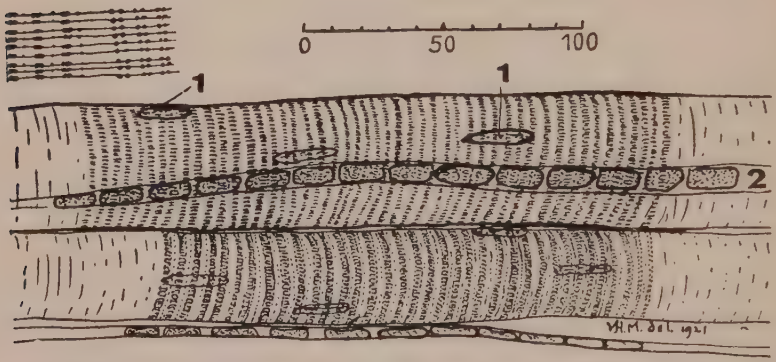



FIG. 51.—Two skeletal muscle fibres with accompanying capillaries. Above, to the left, two interpretations of the way in which the cross-striations are formed. $\frac{1}{6}''$ × 2. C.

1. Nuclei. 2. Capillary with red blood corpuscles.

even as much as 36,000$\mu$, though it will be seen from this that no one fibre runs the whole length of a muscle. The ends of the fibres are rounded and either are inserted straight into a tendon (see fig. 198) or end blindly in close apposition to a neighbouring fibre. In transverse section each fibre is polygonal and usually one, two, or even more nuclei will be seen immediately under the surface (fig. 52). The body of the fibre is granular in appearance, which is due to there being fibrils, cut transversely, running in a mass of undifferentiated protoplasm, called the sarcoplasm. The areas formed by the fibrils are called, after their discoverer, Cohnheim's areas.

On looking at a teased preparation, or a longitudinal section of a muscle under the high power, we notice, first of all, the large number of nuclei in each muscle cell. (In a length of 100$\mu$ there may be three nuclei, and so in 36,000$\mu$ there will be over 1,000 *nuclei in one muscle cell.*) Second, a large number of capillaries, three or four to each fibre, will be seen, and thirdly, a cross-striation, which is so characteristic of these muscles (see figs. 51 and 65).

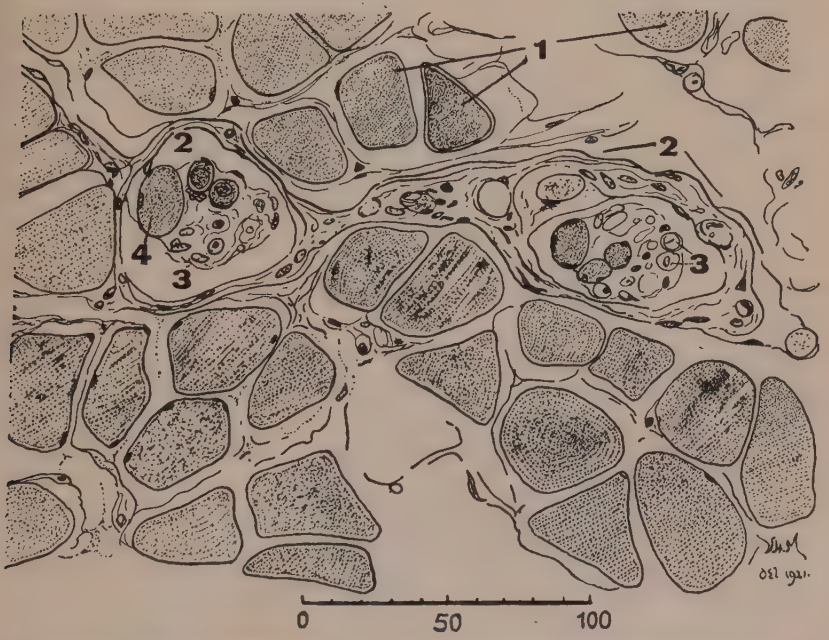



FIG. 52.—Transverse section of skeletal muscle fibres and two muscle spindles. $\frac{1}{6}$" × 2. G.A.H.

1. Muscle fibres showing fibrils cut transversely. Their nuclei are to be found at the angles of the prisms. 2. Muscle spindles, with a connective tissue sheath externally and, internally, 3, medullated nerve fibres, and 4, smaller muscle fibres.

The cells are uniform in thickness throughout their length, and unless it be in the tongue muscles there is no branching of the fibres, nor anastomoses. Each cell is a separate entity. Over each cell is a tough membrane, called the sarcolemma, which can usually be demonstrated by crushing a muscle fibre with a bristle and fixing and staining the result with

van Gieson. The sarcolemma appears stained magenta, whereas the muscle substance is brownish orange. This sarcolemma is continuous with the tissue of the tendon, and so forms a link of union between muscle and tendon. Muscle fibres can be broken up into two sets of elements : (1) discs, or transverse elements, each corresponding to a cross-striation ; and (2) longitudinal elements, or fibrils, each corresponding to a Cohnheim's area in transverse section, or to the faint short longitudinal lines which go to compose the cross-striations (see figs. 51 and 65).

As to the ultimate structure of muscle and its bearing on the theories of muscle contraction, there is little that concerns the elementary student. There is a multiplicity of names given to the various appearances seen under extremely high magnification. As much as the student can see is that each cross-striation consists of a number of parallel short longitudinal lines, with a thin dotted line between each major cross-striation (see fig. 51). By different methods of fixation and different levels of focusing, different interpretations of what is really there and what is seen can be made. In the figure a drawing is given of the general appearance of the muscle fibre, and above, to the left, two "interpretations" of the cross-striation are shown, first from one part of the fibre and second from an adjacent portion.

**Unstriped Muscle**—The best impression of what an isolated unstriped muscle fibre looks like is obtained from a preparation of the frog's bladder (see fig. 53). The cell is a very elongated spindle, almost hair-like in appearance, at least 200$\mu$ in length. At the middle of the hair-like cell is a swollen portion about 20–30$\mu$ long, containing an ovoid to rod-shaped well-staining nucleus. The nucleus has a well-defined chromatin network, and in the protoplasm, close to the centre of the nucleus, may be found two centrioles. Beyond each end of the nucleus the protoplasm is granular.

Unstriped muscle fibres in such isolation will be found nowhere else by the student, unless the muscle coats of (say) the intestine be taken and teased very carefully. Isolated cells there have a general resemblance to those found in the frog's bladder. They are more fusiform, more spindle-shaped, and not so hair-like, and the nuclei are more oval. But it is the appearance of the unstriped muscle in bundles that more concerns the student. Unstriped muscle enters into the

structure of a great many of the organs that most interest him, and it is their arrangement, whether in two or three distinct layers, whether oblique or longitudinal or circular, that enables him to identify organs under the microscope.

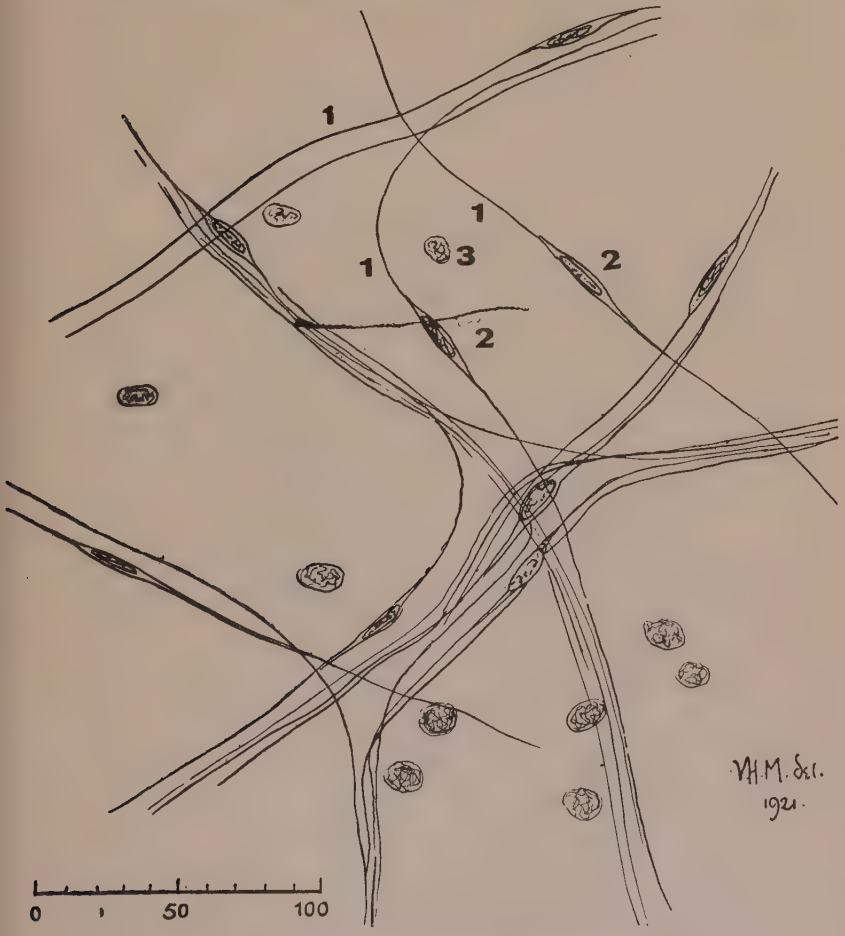



FIG. 53.—Visceral, or unstriped muscle fibres. (Frog's bladder.) $\frac{1}{8}'' \times 2$. C.
1. Muscle fibre. 2. Nucleus. 3. Lamellar cells of the connective tissue of the bladder.

In transverse section the fibres are seen to be grouped into bundles, and these bundles vary much in size and the number of fibres they contain (see œsophagus, fig. 170; uterus, fig.

179; large intestine, fig. 89). Under the low power each fasciculus (bundle) will show one or two or more darkly staining spots in the midst of a number of much smaller and more lightly stained spots. The former are the nuclei of the cells cut across, and the latter the extranuclear part of the cells. Naturally, the latter are more numerous. Under a high power (see fig. 54) the nucleated portion of the cell is seen to be circular to elliptical, and measuring at the greatest diameter about 5$\mu$. The fibres elsewhere may be as little

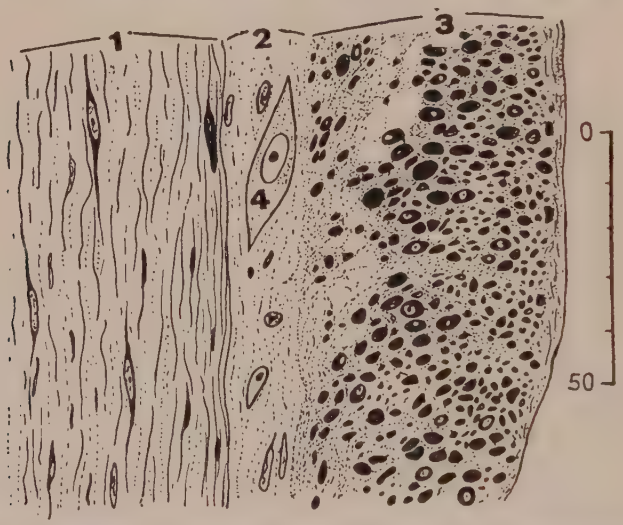



FIG. 54.—Visceral, or unstriped muscle *in situ* in the small intestine. $\frac{1}{8}$" × 4. C.

1. Circular coat of muscle fibres cut longitudinally. 2. Connective tissue in between the two coats, with a nerve cell of Auerbach's plexus. 3. Outer, longitudinal coat of muscle fibres cut transversely. The muscle fibres appear as black dots of various shapes and sizes, except where cut through the nuclei. 4. Nerve cell of Auerbach's plexus.

as 0·5$\mu$ across (see also fig. 172, which contrasts striped and unstriped muscle in cross-section).

In a longitudinal section the bundles of unstriped muscle fibres appear very much as might be expected if hundreds of single fibres be placed side by side with little regard to the disposition of the nuclei except that they be not side by side. Sometimes the nuclei of adjacent fibres are arranged *en échelon*, but usually they are scattered in a haphazard way.

When single unstriped muscle fibres are teased from an

artery they are seen to depart considerably from the typical spindle-like form ; they are irregular in shape, flattened and crumpled—something like a shrivelled autumn leaf. In the intestine the cells frequently show, in the fixed preparation, knotted condensations of the protoplasm which produce, if, as is normal, adjacent fibres are knotted in the same position, an appearance of an irregular transverse striation over the whole of the bundle. In the uterus the individual fibres

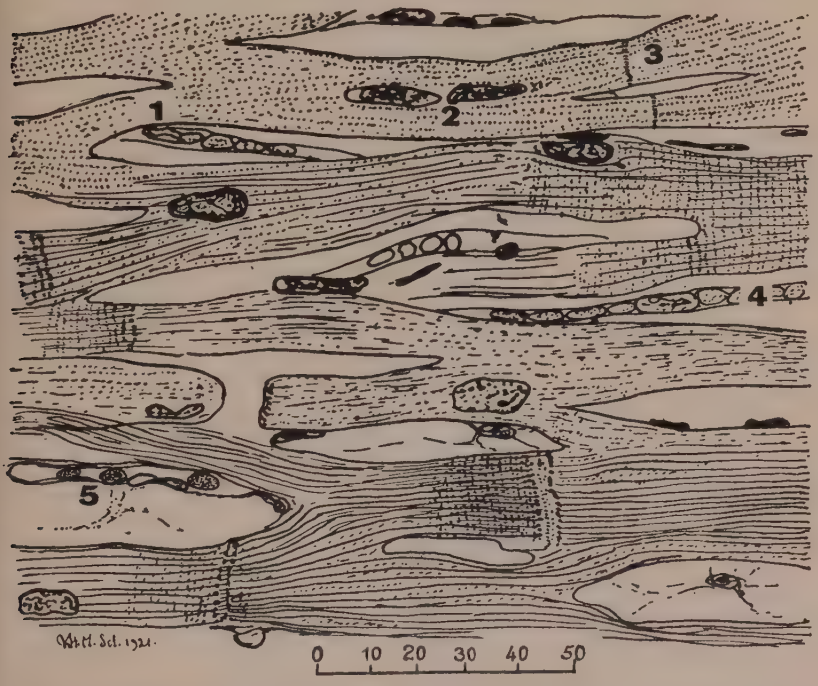



FIG. 55.—Cardiac muscle fibres cut parallel to their length. $\frac{1}{8}$" × 4. G.A.H.

1. Anastomosis of fibres. 2. Nuclei of fibres. 3. Septa between fibres. 4. Capillary with one white and several red corpuscles. 5. Capillary showing nucleus of its wall and three red corpuscles.

are six times as long during pregnancy as during the resting stage.

An interesting contrast between the appearance of striped and unstriped muscle may be seen in the upper part of the œsophagus (fig. 172), where both types are seen side by side.[1]

[1] A useful guide in deciding from which part of the œsophagus the section is taken.

**Cardiac Muscle**—This type of muscle occurs in the heart only. The cells are comparatively short (fig. 55), and are smaller in diameter than those of striped muscle. The protoplasm of the cell is striated, much like that of striped muscle, but more faintly. There is, however, but one nucleus to each cell (rarely two), and this nucleus is placed centrally, in the heart of the cell, and not at the periphery, as is the case with

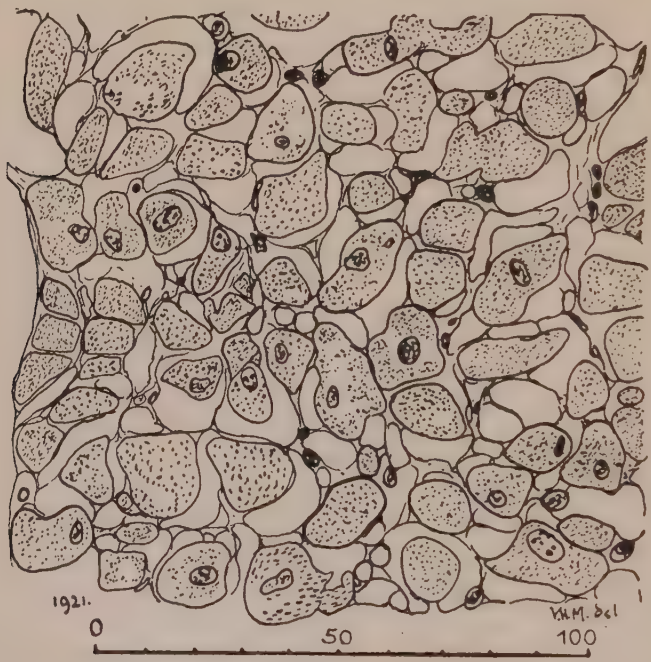



FIG. 56.—Cardiac muscle cut transversely to the fibres. $\frac{1}{8}$" × 4. G.A.H.

The nuclei are well within the cell (compare skeletal muscle fibres, Fig. 52); the fibrils appear as round dots except where the fibre runs obliquely, when they appear as short rods; there is a large amount of space between the fibres and very many capillaries.

striped muscle. This is well seen in transverse section (fig. 56, which compare with fig. 52).

The nucleus is oval to rod-shaped and stains well, containing a network of chromatin. There is a prominent nucleolus. Below and above the nucleus is a long strip of undifferentiated —i.e. unstriped—protoplasm, often granular, and in pathological states, with scattered fat globules. Moreover, there is considerable anastomosis between the different cells, small

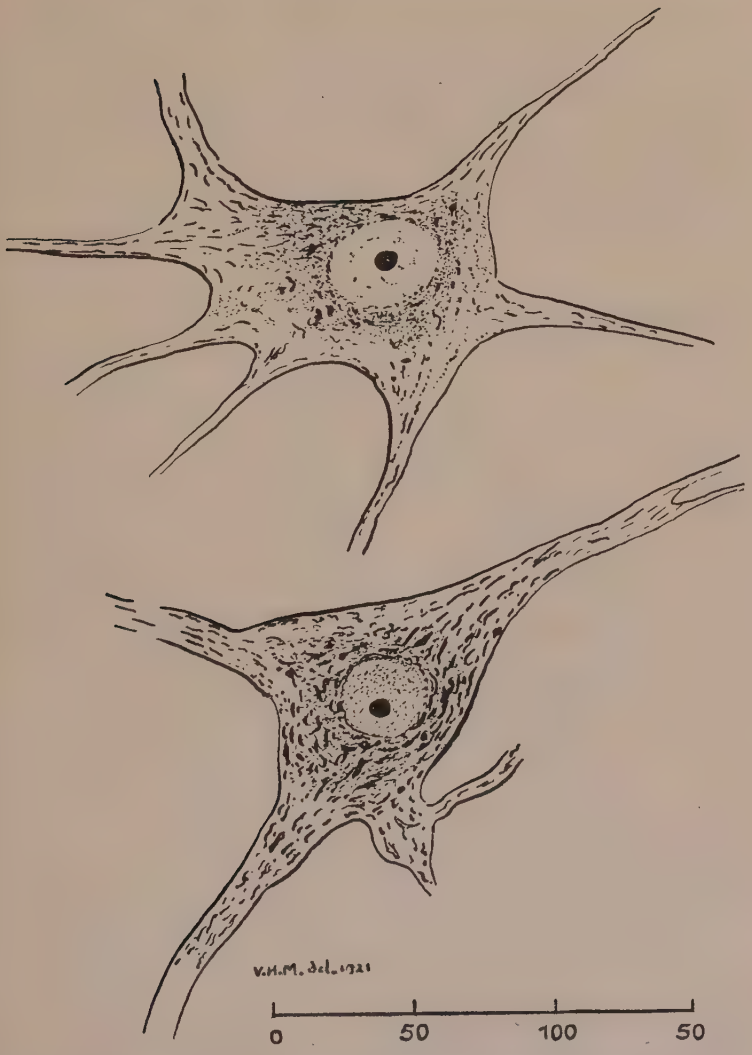



FIG. 57.—Nerve cells from a smear preparation of spinal cord. $\frac{1}{6}$″ × 2. C.

projections passing from the head of one cell into its neighbour.[1] In this way physiological continuity between cell and cell

[1] This feature gives rise to the " coffee-pot " appearance of cardiac cells, described by most textbooks, and looked for, but rarely found, by the student.

is obtained, and morphologically cardiac muscle is distinguished from skeletal and unstriped muscle. The cells are separated by septa, stainable by silver nitrate, but there is evidence that the fibrils (closely comparable to those of skeletal muscle) bridge these septa and so bring each cell into continuity with its neighbour. This is especially striking in the fibres of the bundle of Purkinje, which are embryonic muscle fibres, used for the conduction of impulses from auricle to ventricle.

## NERVOUS TISSUE

Nervous tissue consists of two things, namely, nerve cells and their processes. Unfortunately the term nerve cell, which should logically be applied to the unit which comprises the body and its projections, has come to mean simply the cell body without its processes. The term neuron has been adopted to indicate the whole unit. Perhaps it would be more logical to adopt the term cell body or perikaryon for the part we call the nerve cell, but ordinary nomenclature is so established that it would be too difficult a task to upset it.

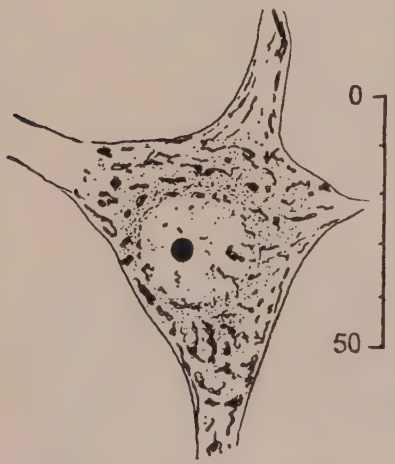



Fig. 58.—Anterior root nerve cell from section of spinal cord. $\frac{1}{8}$″ × 4. W.M.C.
Note the absence of Nissl's granules from one of the branches, i.e. the axon.

The appearance of the nerve cell is very varied indeed, both in size and in the arrangement of its parts. In each, we may see that the cell has proportionately a very large nucleus in which there is little chromatin visible. There is a large nucleolus to each nucleus. The cell body may be rounded (see fig. 60), or star-shaped (figs. 57 and 58), or flask-shaped (fig. 59), or cigar-shaped. Indeed, it is protean in shape and size: its dimensions run from 2$\mu$ to 100$\mu$. Its protoplasm is granular, containing round shining granules when seen in the living state under dark-ground illumination. When fixed, particularly with fixatives containing mercury

chloride, there are granules which stain deeply with methylene blue, named after their discoverer, Nissl's granules (figs. 57 and 58). These granules are almost undoubtedly artefacts, that is, they correspond to little that is there in real life, but they serve to indicate the state of functional activity of the

FIG. 59.—Purkinje nerve cells from the cortex of the cerebellum. G.A.H. Above, to the right, a small scale drawing from the same region.

cell. In a resting unfatigued cell there are numerous Nissl's granules. In a fatigued cell or a cell that has been damaged they disappear. Fibrillation has also been described in the nerve cell, but it is doubtful, again, whether this fibrillation exists in real life. Probably it has been produced by the method of fixation.

The nerve cell usually has numerous processes projecting from it. But the cells of the sensory ganglia have one only, and other cells, such as those in the retina, and the olfactory cells have two only. The first are termed monopolar, and the second bipolar. But when we look at a cell such as those of the cerebral cortex (see fig. 62), or the motor horn (anterior column) cells of the spinal cord, we see that each cell has four or five or more processes. Some of these are fine and very much branched. They are spoken of as dendrons. There is one process which is different from all the others. In the first place, Nissl's granules do not extend along it, in the second place it proceeds to some very considerable distance. For instance, this process, called the axon, may proceed from a cell in the cerebral cortex right down throughout the length of the spinal cord. The function of the branches, that is the dendrons and axon, is to keep the nerve cell in, or to bring it into communication with, other nerve cells, or with sense organs, or with effector organs, throughout the body. The function of the cell-body is trophic, i.e. to keep the axons and dendrons alive and active.

For types of the nerve cell, we may take :

(1) **The motor cell**—This cell is to be found in the grey matter of the spinal cord, in the anterior column or horn. The largest and best examples to be seen are in the cervical and the lumbar swellings : these cells activate the muscles of the limbs. They are star-shaped, measuring 50–100$\mu$ across, have large nuclei with very little chromatin, and a large nucleolus within the nucleus. The protoplasm shows Nissl's granules. The arrangement and size of such depend to a great extent on the method of fixation. These granules are seen within the dendrons and are absent from the axon (fig. 58).

(2) **Sensory ganglion cells** (fig. 60)—These cells are round, and measure 50–70$\mu$, have a fairly large nucleus, say 30$\mu$ across, and a marked nucleolus. They have one process (axon) only, which branches at some distance from the cell into two. One branch extends from the periphery of the body to the bifurcation, and the other from the bifurcation into the central nervous system. These cells were originally bi-polar, and are still so in fishes, but it has appeared useful to remove the cell from the main line of communication and put it on a side branch.

(3) **Pyramidal cells** (fig. 62)—These cells are found in

the cortex of the brain, and are largest in the motor cortex (fig. 224). Their name suggests their shape, i.e. of a pyramid. From the vertex of the pyramid, a long branched dendron passes up towards the exterior of the cortex. From the other angles, dendrons pass out horizontally. From the base, an axon passes from the cortex down to the motor cells in the

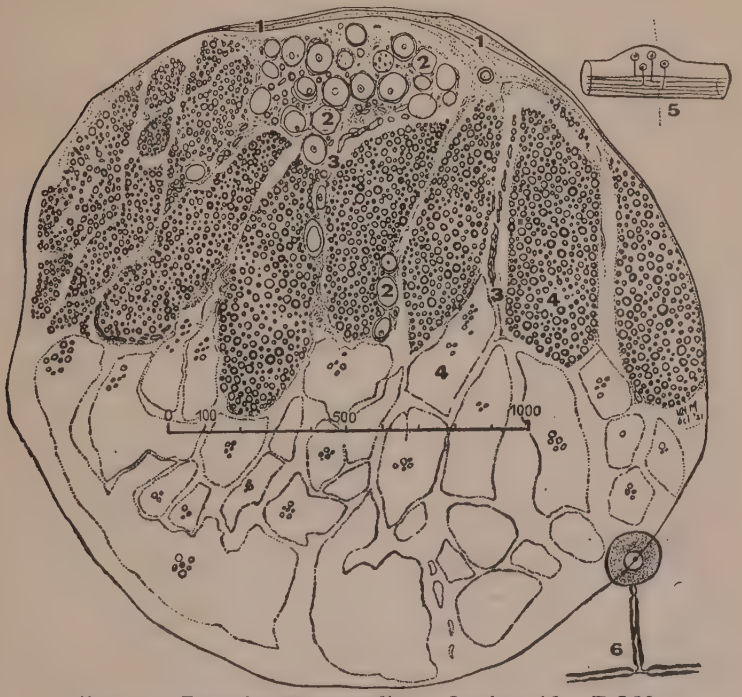



FIG. 60.—Posterior root ganglion. Osmic acid. E.C.M.

1. Connective tissue sheath continuous with epineurium. 2. Ganglion cells of posterior root ganglion. 3, 3. Nerve fibres, cut longitudinally, passing up towards the ganglion cells. 4, 4. Bundles of nerve fibres, roughly corresponding to the funiculi of the nerve trunk, cut transversely. 5. Diagram of the position of the section in the ganglion. 6. Diagram showing relation of a nerve cell of the ganglion to its fibre.

lower parts of the C.N.S., to make communications between those cells and the cells which initiate the nervous impulses which cause movement.

(4) **Purkinje cells** (fig. 59)—The cells are flask-shaped, have a large axon passing centrally and peripherally, an enormous ramification of dendrons greater than that anywhere else in the body. They are found in the cortex of the cerebellum.

(5) **Sympathetic ganglion cells** (fig. 61)—These cells are multi-polar, that is, they have an axon and several dendrons. The cell body is angular or star-shaped, the axon differs from the ones we have seen so far, in obtaining no medullary sheath (see later). In some animals the cell body contains two nuclei.

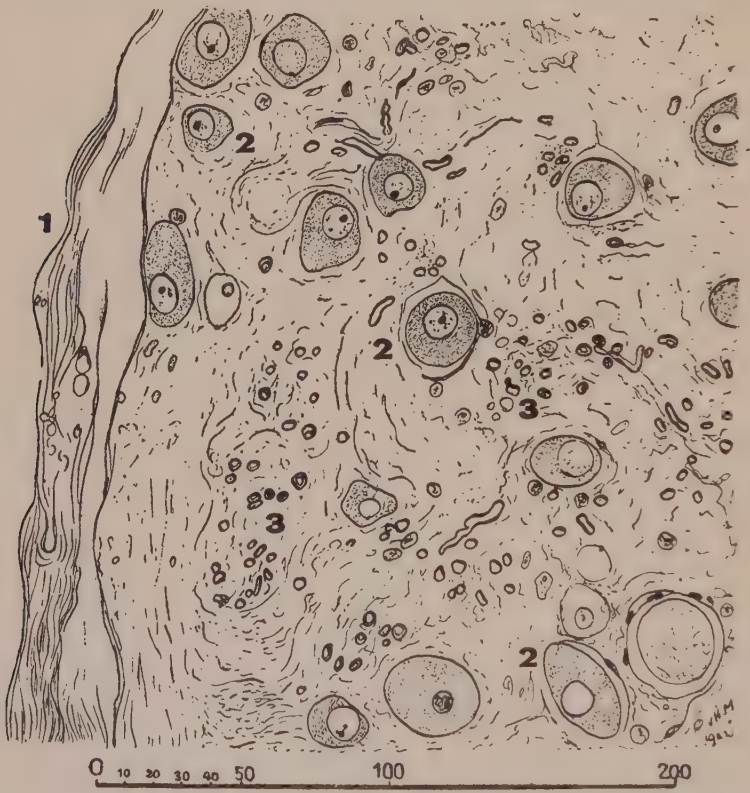



FIG. 61.—Sympathetic ganglion. Preparation fixed with osmic acid. $\frac{1}{8}''$ × 2. A.B.W.

1. Connective tissue sheath over ganglion. 2. Ganglion cells, the largest of which is not 40$\mu$ in diameter. 3. Small medullated fibres, the diameter of which is about 2$\mu$. (Compare sensory ganglion, Fig. 60.)

**Types of Axons**—Axons, or nerve fibres, can be classified as follows:

(1) Large medullated.
(2) Small medullated.
(3) Non-medullated.

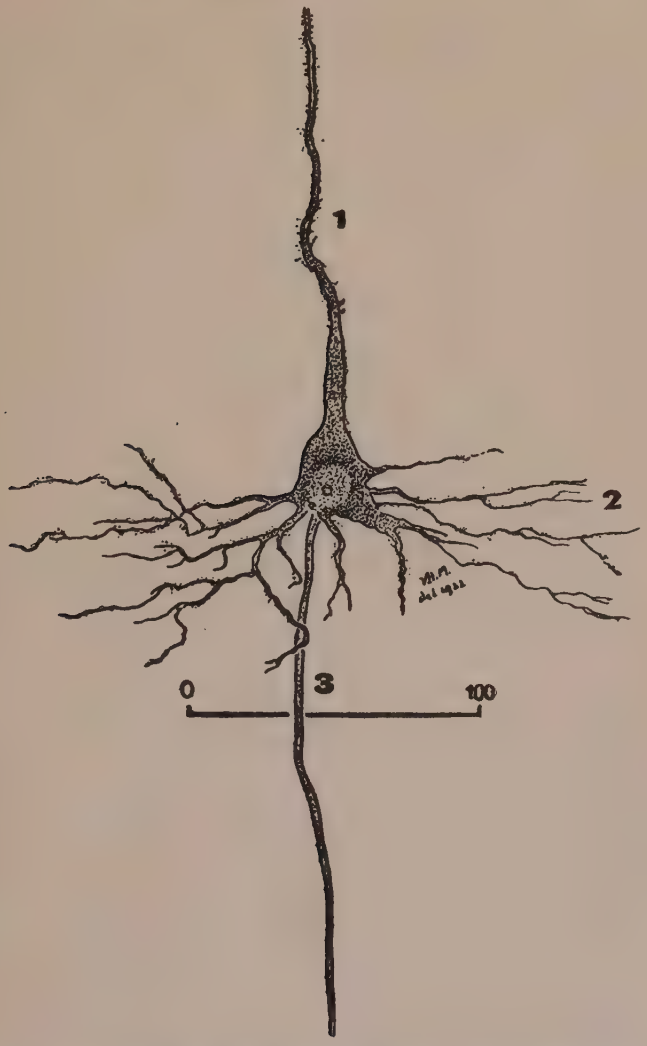



FIG. 62.—Pyramidal cell from cerebral cortex. Golgi preparation—the precipitation being rather light. $\frac{1}{8}'' \times 2$. C.

1. Apical dendron passing out to the outer layers of the cortex, and cut short. 2. Basal dendrons. 3. Axon passing towards the white matter of the brain.

When a nerve is teased into its ultimate parts, the units are seen to consist of long strands, with here and there a constriction called a node of Ranvier (fig. 63). The distance

between nodes varies—near the cell it is great, comparatively speaking : in those shown in the figure the internodal distance

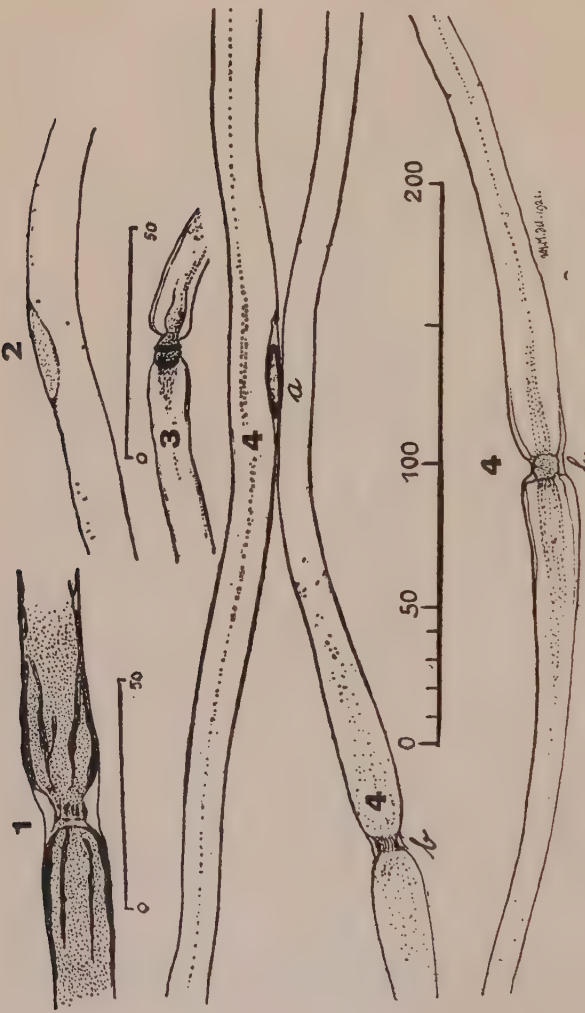



FIG. 63.—Large medullated nerve fibres teased from mixed nerve. C.

1. Node of Ranvier stained with silver nitrate. 2. Nucleus of neurolemmar sheath (silver nitrate preparation). 3. Node of Ranvier (silver nitrate). The silver nitrate has penetrated some way along the axis cylinder. 4. Three fibres teased, fixed, washed with chloroform and ether to dissolve the medullary sheath, and then stained with hæmatoxylin. $\frac{1}{2}$ × 2. *a*. Nucleus of neurolemma half-way between two nodes. *b*. Nodes of Ranvier.

was 1,000$\mu$. Nearer the peripheral terminations the internodal distance may be 50$\mu$ only (figs. 65, 197 and 198).

Over the nerve fibre is a fine sheath called the neurolemma,

and in this sheath, half-way between the nodes, is a nucleus, spindle-shaped or oval. Immediately within this neurolemma is a sheath consisting of lecithin, called the medullary sheath. This is interrupted at each node. The medullary sheath stains black with osmic acid, because it contains a reducing fatty acid. Internal to this medullary sheath is a strand of tissue, apparently fibrillated, called the axis cylinder, which passes the whole way from the nerve cell down through the nodes of Ranvier to the periphery. Sundry breaks have been described in the medullary sheath, but it is probable that these are the result of fixation. At the junction of the internodes there is cement substance (staining black with silver nitrate, and producing the well-known crosses in nerve fibres), which serves to unite each neurolemma cell with the next.

The description given above applies to both large and small medullated nerve fibres, the large medullated fibres running from 10–20$\mu$, while the small fibres are 2$\mu$ only. The large fibres belong to skeleto-motor and sensory nerves, whereas the small medullated fibres belong to viscero-motor nerves.

**Non-medullated Fibres**—These fibres, at first sight, look like small medullated fibres, which have lost their medullary sheath. There is a small axis cylinder, and perhaps a neurolemma. The sheath over each fibre has nuclei interpolated on the course of the fibre. In transverse section they appear remarkably like a transverse section of unstriped muscle, and are best distinguishable from that by the regularity and size of the fibres. They will frequently be found present in nerve bundles, for example in the posterior root (fig. 64).

The importance of the medullary sheath in a medullated nerve is apparent from the facts: (1) a medullated nerve does not become functional till it receives its medulla; (2) a medullated nerve ceases to conduct if the medulla breaks up as the result of either disease (e.g. polyneuritis) or section of the nerve with consequent degeneration of the part of the axons cut away from the cell.

This degeneration, which occurs throughout the distal portion and in the central portion up to the next node, is known, after its discoverer, as Wallerian degeneration. The stages of the process are as follows:

(*a*) Within twenty-four hours the neurolemma becomes more visible, the nuclei start multiplying and the protoplasm hypertrophies.

(*b*) The medullary sheath begins to break up, and its continuity is completely severed. (At this stage the nerve ceases to transmit impulses—about four days after section.)

(*c*) By the fifth day the medullary sheath has completely broken up into drops, and the axis cylinder consists of short masses of fibrils only.

(*d*) The drops of myelin [1] almost completely disappear, together with the remains of the axis cylinder. Probably the myelin is removed by leucocytes, for cells around the degenerating nerve increase their fat granules (five to twenty days).

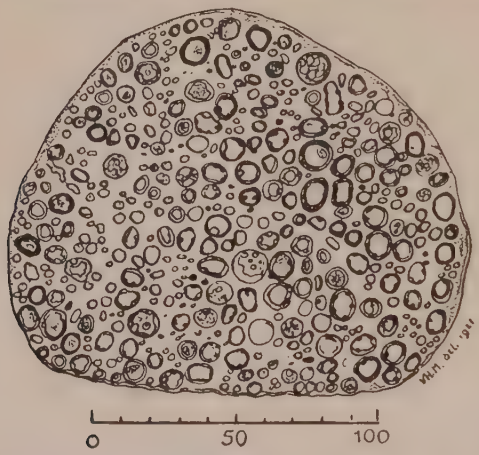



FIG. 64.—One rootlet of a spinal nerve root. Osmic acid. $\frac{1}{6}$" × 2. C. Externally, there is a thin connective tissue covering, and within this large and small medullated and some non-medullated fibres.

(*e*) The final result is a chain of neurolemma cells, with many nuclei: all traces of axis cylinder, and practically all traces of medullary sheath having disappeared. The endings of the nerve, whether motor or sensory, degenerate at the same time, or even earlier than the nerve trunk itself.

Regeneration takes place from the central end of the cut nerve and *outside* the central nervous system only. Damage to a nerve fibre within the central nervous system is never repaired. Axis cylinder fibres grow out from the undamaged part of the nerve, find their way into the neurolemma tubes of the degenerated nerve, and proceed to grow down them.

[1] Myelin: the name for the substance of which the medullary sheath is composed.

Sometimes they do not find their way and wander along damaged muscle, or in between the neurolemma sheaths. In the latter case a neurolemma sheath is formed round them, and a new nerve fibre results. The stages of regeneration are the reverse of the stages of degeneration, myelin is deposited,

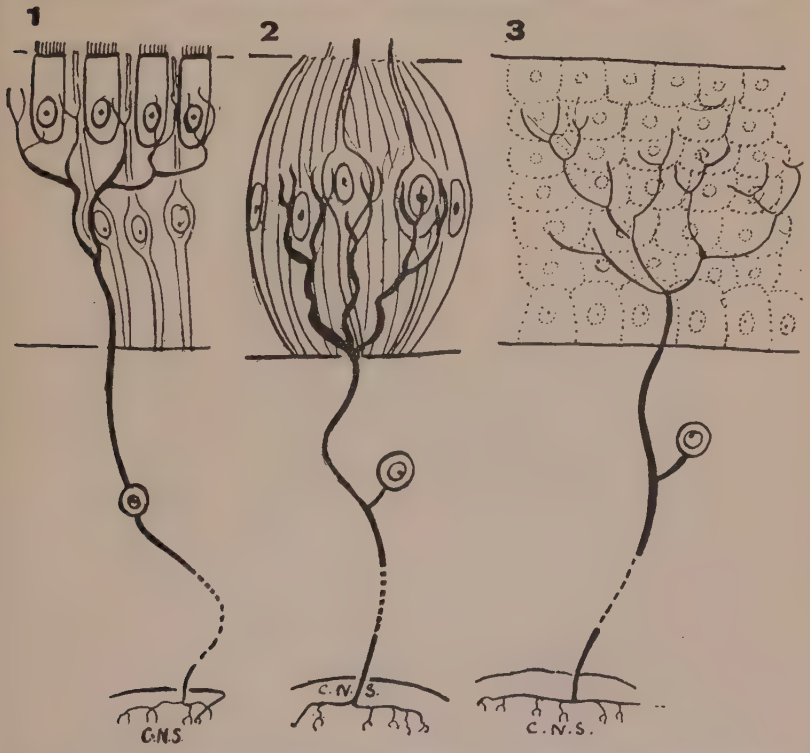



FIG. 65.—Three sensory nerve-endings similar in design. The sensory nerve fibre branches and ends *between* epithelial cells.

1. Auditory nerve-endings. 2. Gustatory nerve-endings. 3. Tactile.

the axis cylinder is formed, the medullary sheath is completed, and the nerve starts to function. The process is very slow. The beginning of regeneration takes sixty to seventy days. Functional continuity is rarely observed before the hundredth day, and, in man, complete functional activity may not be restored till a year's time.

Both sensory and motor nerves have to make connections either with other nerve cells or their dendrons (synapses),

or with the sensory organs or effector (muscle or gland) organs with which they communicate. There is much evidence (physiological and pharmacological) that these synapses and endings differ chemically in their nature from either the cell or axon. (See effects of curare, nicotine, gymnema, menthol, cocaine and other anæsthetics, local and general, on nervous

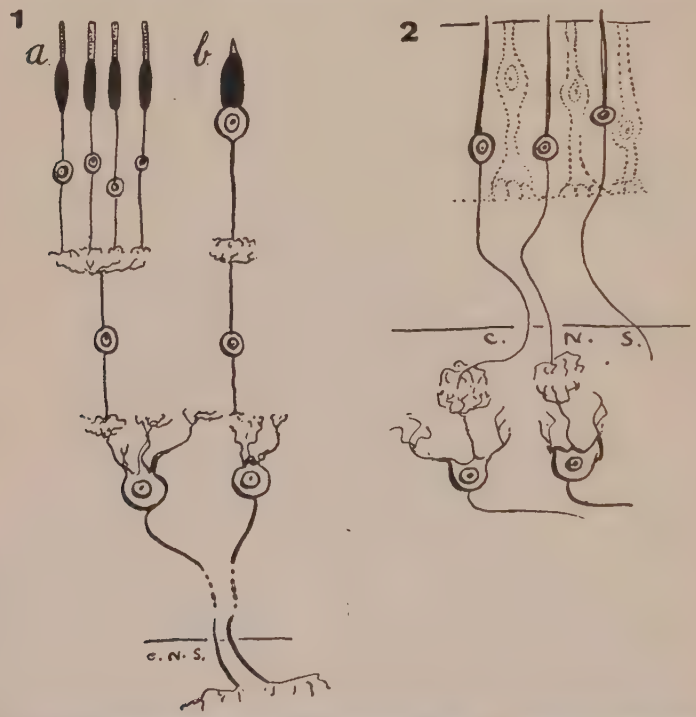



FIG. 66.—Sensory nerve-endings of a second type. The specialized sensory cell is a nerve cell. (Cp. the endings in 65, where the specialized cell is in 1 and 2 an epithelial cell.)

1. Visual nerve-endings in the retina. *a*. Rods. *b*. Cone. 2. Olfactory nerve-endings in olfactory mucous membrane.

tissue in any pharmacological textbook.) This difference is correlated with great difference in the endings.

The discussion of sensory endings it will be convenient to postpone until the discussion of the sense organs from which they run is taken up, except to say: (1) the medullation of the fibre begins *after* the nerve leaves its sensory organ, except in the olfactory nerve and in the short processes of the rods

and cones of the retina, which are homologous with sensory nerves. These are never medullated. (2) The ending of the nerve may be of several types :

(*a*) Simple blind endings after considerable branching among peripheral cells. Fig. 65.

(*b*) Flowered or beaded, or ivy-leafed endings among connective tissue fibres.

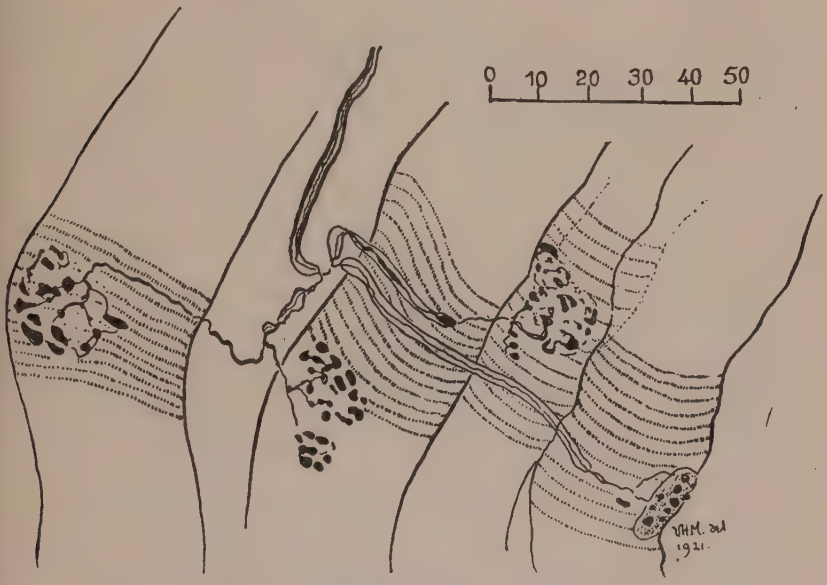



FIG. 67.—Motor nerve-endings in skeletal muscle. $\frac{1}{8}$″ × 4. C.

The nerve fibre, which is medullated and rather small, branches into four and supplies four muscle fibres. Note that the branches lose their medullary sheath some little distance before they reach the endings.

(*c*) Plaque-like endings around epithelial cells in hairs and special tactile organs, such as those of the pig's snout.

(*d*) Plaques and flowered endings between specialized epithelial or connective tissue cells, as in Grandy's and Herbst's corpuscles, Meissner's sense organs (figs. 194 and 195) and Pacinian corpuscles (fig. 196).

(*e*) Annular and spiral endings around muscle fibres in muscle spindles (fig. 197).

**Motor Nerve Endings**—These are simple in unstriped and cardiac muscle. The efferent fibre branches repeatedly at

right angles to its main course, giving off very fine branches. These run along parallel to the direction of the muscle fibres, and eventually end in close apposition to them in fine tapered endings, or in bulbous extremities. A network formed by anastomosis of the fibrils is seen in the cardiac muscle and in blood vessels.

In voluntary muscles there is an organ known as an end-plate (fig. 67). The nerve fibre courses to the muscle fibres and divides into three or four branches at a node. The branch about to give rise to an ending loses its medullary sheath and enters the end-plate. This is a thin disc applied to the surface of the muscles, in which a ramification of the axis cylinder takes place with the formation of flowered endings. Underneath this end-plate, nuclei (not shown in the figure) have been described.

When nerve cells are massed in well-defined groups, the groups are called ganglia. There are ganglia both within and without the central nervous system. Those outside occur: (1) on the sensory roots of sensory nerves close to the central nervous system, e.g. the Gasserian ganglion or posterior root ganglion; (2) on the course of viscero-motor nerves on their way out to the periphery, e.g. the submaxillary ganglion, Langley's ganglion, the ganglia of Bidder and Remak, the ganglia of the sympathetic chain.

**Sensory Ganglia** (fig. 60)—The ganglion is enclosed in a strong fibrous connective tissue sheath, continuous with that of the nerve on which it is placed. Strands from this sheath pass in between the nerve fibres, dividing them into groups or bundles. To one side of the ganglion the nerve cells appear. This is somewhat exaggerated in the diagram, for the section is made near the end of the ganglion and not through its centre. Often half or more of the ganglion consists of nerve cells, but nearly always (unless the section passes tangentially and longitudinally to the ganglion) the cells are markedly to one side of the preparation. Fibres can be seen passing up from the main mass of nerve fibres, to connect with the nerve cells. The interpretation of this is seen in the small diagrams accompanying the figure. Each fibre connects by a T-piece to one cell. Around each cell is a spherical nucleated capsule continuous with the neurolemma sheath of the nerve fibre. The nerve cell contains one nucleus only, and measures approximately 70$\mu$ across. The nerve fibres are nearly all medullated and large (10–15$\mu$).

**Sympathetic Ganglia** (fig. 61)—The main differences between sensory and viscero-motor ganglia are that the latter: (*a*) have a smaller size; (*b*) the cells are scattered among the fibres, and are not to one side; (*c*) the cells are smaller—30–40$\mu$; (*d*) there are often two or three nuclei to a cell; (*e*) the fibres are small (2$\mu$) and many of them non-medullated;

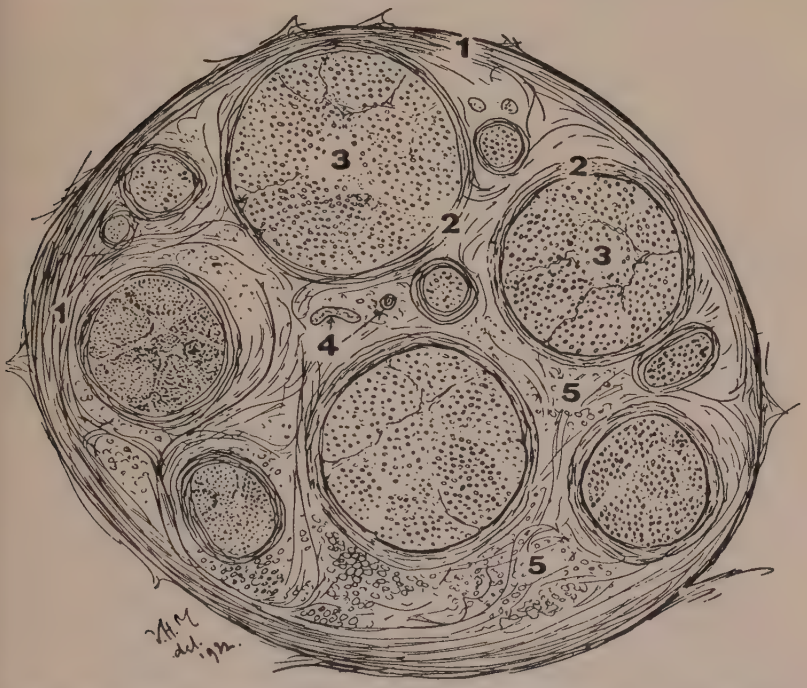



FIG. 68.—Rough sketch of nerve trunk in transverse section. (Cp. Fig. 60.)

1. Epineurium of connective tissue covering the nerve trunk, connecting it with other connective tissue in the neighbourhood, penetrating in between the various funiculi, carrying blood vessels and nerves and containing adipose tissue. 2. Perineurium of connective tissue covering each funiculus and penetrating between the bundles of nerve fibres in the funiculi. 3. Funiculi. 4. Blood vessels. 5. Adipose tissue.

(*f*) the capsules over the cells are not so spherical. Otherwise there will be seen to be not much difference between the two types of ganglia, unless one resorts to teasing them or to functional tests.

It is usually convenient to the body that the nerve fibres running between one part and another should run in groups.

Inside the central nervous system these groups are termed fasciculi[1] (see later), and all the fibres of one fasciculus have the same function. But outside the central nervous system this is by no means necessarily so. The grouping of nerve fibres into bundles is based more on convenience than on function, and the groups need considerable protection and ligation by connective tissue.

If we take a large nerve, such as the sciatic, and make a cross section, we find that over the whole, and running between bundles of nerve fibres, we have a strong connective tissue sheath called the epineurium (cf. muscle). This epineurium often contains adipose tissue (fig. 68), and in it run fairly large blood vessels. The bundles of nerve fibres (termed funiculi[2]) may be large or small, according to the number of fibres within them. The funiculi anastomose freely, no one being continuous for long. They interchange fibres where they anastomose, this probably being to distribute the fibres according to their ultimate destination. The individual fibres do not branch. Each funiculus has a circularly arranged sheath of connective tissue, consisting for the most part of white fibres, but having a network of fine elastic fibres within it. Each layer has an epithelioid membrane over it (fig. 13). Within the funiculus is a looser connective tissue called the endoneurium, supporting the individual nerve fibres. The fibres are seen to be of all diameters from 15$\mu$ down to 1 or 2$\mu$, and the majority are medullated (fig. 64). The appearance of the individual fibres varies: (1) according to where they are cut, and (2) according to the fixing and hardening reagents used. It is customary to use osmic acid in the fixation of nerves, and figs. 60 and 64 are from nervous tissue so treated. Ideally there should be seen a black annulus, the medullary sheath, and within this, and centrally placed, a grey axis cylinder. Usually the axis cylinder is seen adhering to one side of the annular medullary sheath, and often the sheath

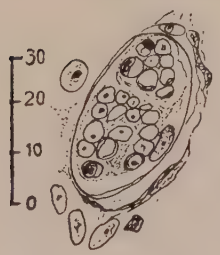



FIG. 69.—Small nerve bundle from mucous membrane of the nose.

The fibres are medullated, but the medullary sheath in most of them has been washed away by the chloroform and xylol used in embedding and mounting.

[1] "Tracts" in the old terminology. Fasciculus = little bundle.

[2] Funiculus = little rope.

is crumpled and beaded, or swollen asymmetrically. If the section passes through the nucleus of the neurolemma sheath, the latter is seen to push the annular sheath into an elliptical shape. Should the nerve have been fixed in other reagents,

FIG. 70.—Nerve bundle treated with ordinary fixatives and stains. $\frac{1}{6}''$ × 2. G.A.H.

Over the bundle is the perineural sheath. The nerve fibres are nearly all medullated, i.e. the nerve was mainly sensory and skeleto-motor.

the medullary sheath remains soluble in xylol and is, in part, or wholly, washed away when mounted in balsam. Then we have such an appearance as in fig. 69, a small bundle of nerve fibres from the nasal mucous membrane, or in fig. 70, from a rat's tail. The fibres of the former have possessed a medullary

sheath, but it has mostly been washed away. Traces of it can be seen in two or three fibres. From this fact we can be sure that they are not branches of the olfactory nerve, but either sensory or (secreto) motor nerves, from or to the mucous membrane. Small bundles of nerves, seen in the ordinary preparations of (say) œsophagus and trachea, or muscle, have

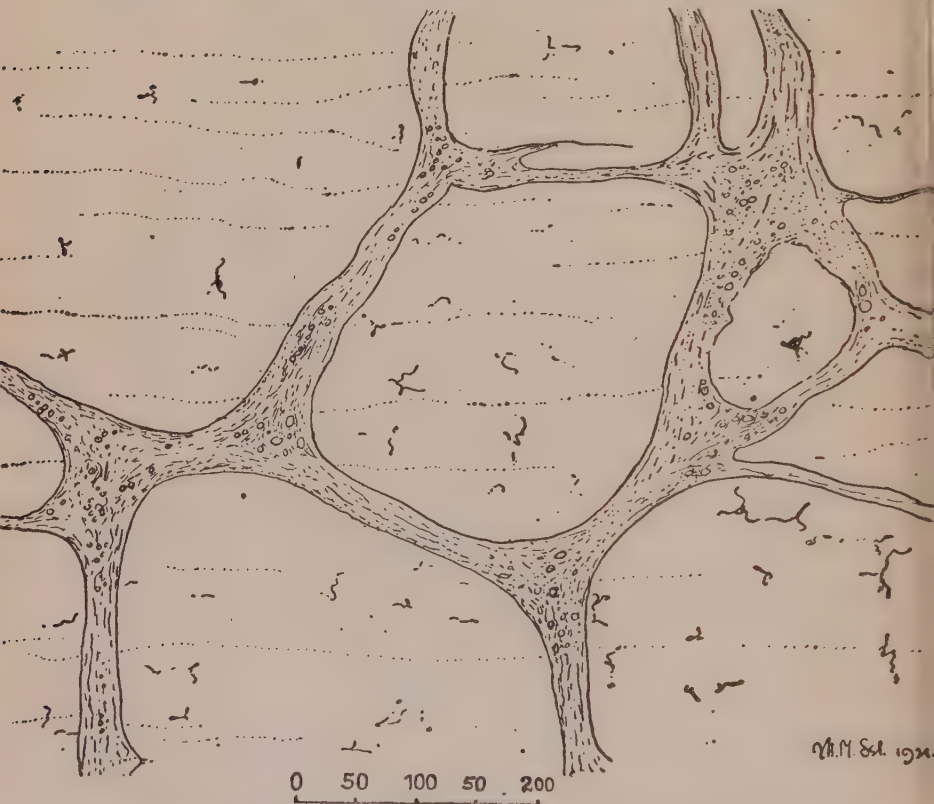



FIG. 71.—Auerbach's plexus. $\frac{1}{8}$" × 4. G.A.H.

The plexus is seen against a background of bundles of longitudinal unstriped muscle fibres, with nuclei of connective tissue corpuscles, etc. Nerve cells are seen in the plexus, more particularly at the junctions or nodes.

much more the appearance of figs. 69 and 70, unless the preparation has been made by osmic acid. The student is warned that a vein with badly preserved red blood corpuscles and a few white corpuscles, a small bundle of unstriped muscle, a non-medullated nerve, or a medullated nerve from which

the medullary sheaths have been washed (as commonly happens) by xylol, may look, at first glance, and even second glance, very much like each other. But an osmic acid preparation of a medullated nerve is so typical that no mistake should be made about it.

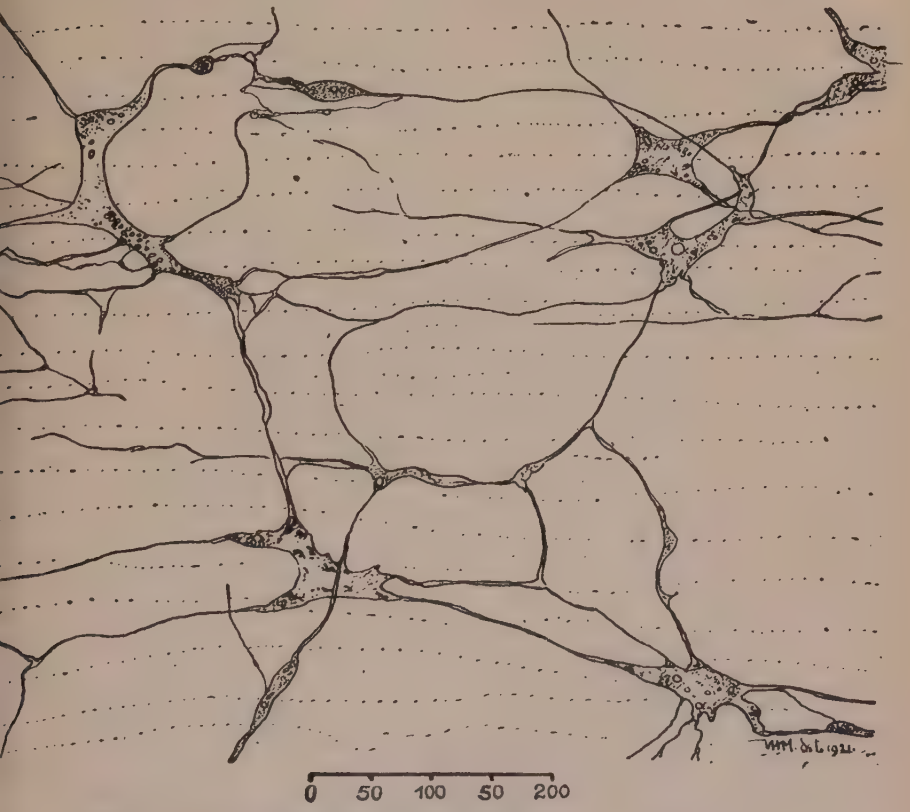



FIG. 72.—Meissner's plexus from small intestine. (Cp. Fig. 71.) $\frac{2}{3}''$ × 4. G.A.H.

The plexus is much finer and more irregular than that of Auerbach.

**Nerve Plexuses**—In between the longitudinal muscle coat and the circular muscle coat of the alimentary tract, and again on the inner surface of the circular coat, lie two nerve plexuses. They are respectively the plexuses of Auerbach and Meissner. Each plexus consists of a network of fibres

(figs. 71, 72), at the knots of which are collected round ganglion cells. The meshwork of Auerbach's plexus is coarser and the cells somewhat larger than those of Meissner. The cells are of the type in which no dendron is especially distinguishable from another, i.e. there is no axon. Each net is connected with the other, and their integrity is essential to the spontaneous rhythmic activity of the gut wall. Such plexuses, which are perhaps representative of the nerve nets of invertebrate animals, are to be found in the alimentary tract only, and form a type of local nervous system, subordinate to, and in the

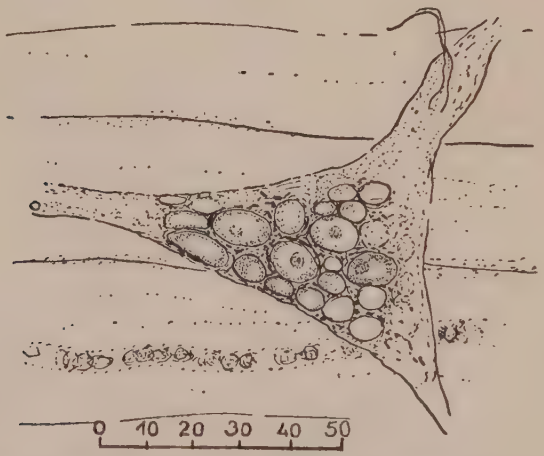



FIG. 73.—Nerve cells at a junction on Meissner's plexus. $\frac{1}{6}$″ × 4. G.A.H.

control of the central nervous system, but able to carry out reflex co-ordinated movements apart from the intervention of the central nervous system.

## THE FREE CELLS

So far, we have been dealing with the elementary tissues, which are, at any rate in the adult, fixed in position. This is true of the cells which are found in them, though potentially some of them are free, and indeed were entirely free in the embryonic state, but there are cells which are free and migratory in adult life. Of these, the most noteworthy are the white and red corpuscles of the blood, the lymphocytes of the

lymph glands, the marrow cells and the wander cells of the areolar tissue. Logically, too, we should place here the spermatozoa and the ova, but the consideration of them will be postponed to a later chapter.

**White Blood Corpuscles**—The classifications of white blood corpuscles have been many: for our purpose a simple, illogical classification—that normally adopted in medicine—is here followed.

(1) Polymorphonuclear.
(2) Eosinophil.
(3) Small and large lymphocytes.
(4) Basophil or mast cells.

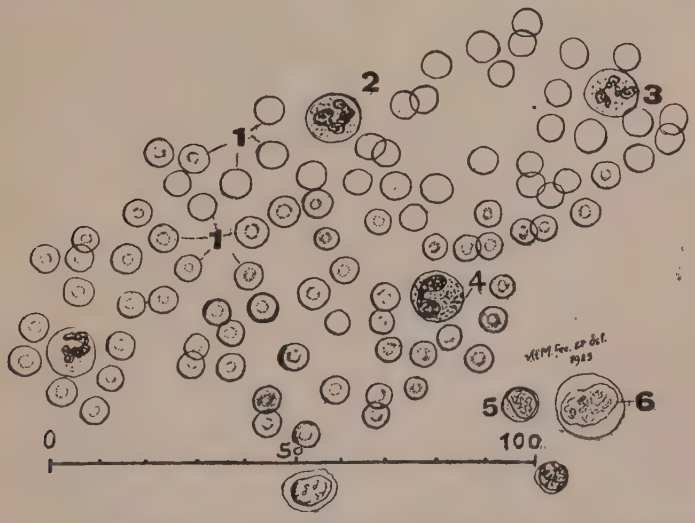



FIG. 74.—Human blood. Film preparation. Stained with Leishman's stain. $\frac{1}{8}'' \times 4$.

1. Red blood corpuscles. 2. Polymorphonuclear white corpuscle. 3. The same, with lobes of nuclei more completely separated. 4. Eosinophil white corpuscle. 5. Small lymphocyte. 6. Large lymphocyte.

**Polymorphonuclear**—These are the most prominent of the white blood corpuscles. They are spherical cells of about 12–15$\mu$ in diameter. The protoplasm is faintly granular, the granules staining with acid dyes, such as eosin. The nucleus, which is brilliantly stained with basic dyes, presents a curious appearance. It consists of one to five lobes, often so nearly separated from one another as to give the effect of separate nuclei. It is thought that the more mature polymorpho-

nuclear cells have five lobes to the nucleus, while the immature ones have a horseshoe-shaped nucleus (figs. 74 and 75 of blood, and 78 of marrow).[1] The chromatin is sharply stained. Sixty-five per cent. of the white blood corpuscles are polymorphonuclear in normal blood, and the average number of lobes is three. When there is much pus formation in the body, as during appendicitis or abscess (e.g. on the teeth or the lungs), there is a large increase in the total number of white blood corpuscles, which run from about 7,000 per cub.

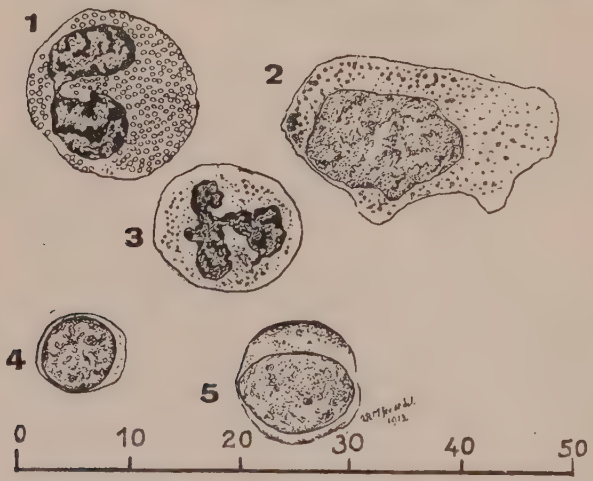



FIG. 75.—White corpuscles from human blood. Film preparation. $\frac{1}{12}''$ × 4.

1. Eosinophil. 2. Large lymphocyte. 3. Polymorphonuclear (lobes not well separated). 4. Small lymphocyte. 5. Small lymphocyte with slightly more cytoplasm than in 4.

mm. to 14,000–20,000, or even more, in such cases. The polymorphonuclear leucocytes in the blood of such a patient form 80–90 per cent. of the total white corpuscles, and the average number of lobes in the nucleus is smaller.

**Eosinophil Corpuscles**—These cells are larger than the polymorphonuclear cells, and contain proportionately larger shining granules, which stain strongly with acid dyes, such as eosin. The nucleus, which stains well with basic stains, is horseshoe-shaped or bi-lobed, but never showing that variety of appearance seen in the polymorphonuclear cells. Its chromatin is sharply stained, as in the case of the latter cells.

[1] See also spleen pulp, fig. 152.

They are rare in the blood, amounting usually to one-half of 1 per cent. of the white blood corpuscles, rarely in the normal blood are there as many as 2 per cent. In bronchitis, asthma, and malaria they increase greatly in number, even 10–15 per cent. may be found.

**Lymphocytes**—Of these there are two varieties, small and large. The small lymphocytes have but very little cell protoplasm, and that with hardly any granulation present; in fact, it is usually clear and hyaline. It stains with basic dyes. The nucleus is round (cp. polymorphonuclear and eosinophil cells), the chromatin is not so marked as in the previous examples, though the nucleus as a whole stains well.

The large lymphocytes are similar to the small, except that there is much more cell plasm, and the nucleus is more faintly stained the larger the cell.

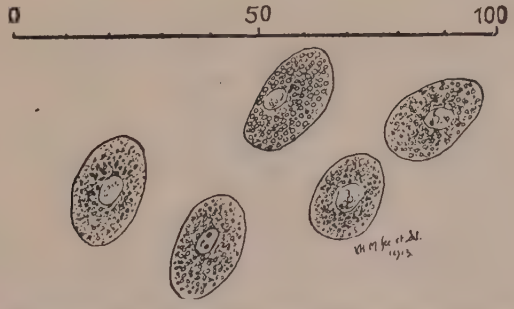



FIG. 76.—Basophil cells from connective tissue of the rat. $\frac{1}{6}'' \times 4$.

Normally, 30 per cent. of the total white blood corpuscles are small or large lymphocytes, the greater proportion being small. These cells are increased in disease of the lymph glands, and are normally much more numerous in infancy.

**Basophil** or **Mast Cells**—Occasionally, but rarely, we meet cells with coarse granules, staining with basic dyes. The number of granules is small, and these stain so deeply with the dye that they look black, somewhat like currants in a currant pudding. In the rat, the cells are oval (fig. 76), contain numerous granules and an ovoid nucleus with a marked chromatin network. In the author's experience they are rarer in normal adults than the textbooks suggest. Often a series of counts of 250 leucocytes each may be made without your seeing a single one.

Sometimes a fifth type of cell, called a transition cell, is seen. This looks like a large lymphocyte, the nucleus of which is notched, as if it were about to turn into a polymorphonuclear cell. Indeed, it has been assumed that the polymorphonuclear cells arise from the lymphocytes, and the transitional cell is a stage in the transition. The lymphocyte arises, in its turn, undoubtedly from the lymph glands.

Another origin has been proposed for the polymorphonuclear cells, and that is the marrow (cf. formation of red blood corpuscle, later), where undoubtedly many polymorphs are

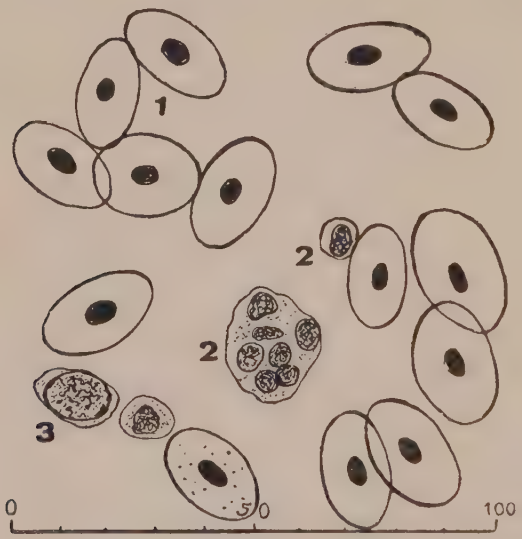



FIG. 77.—Amphibian blood. $\frac{1}{8}'' \times 4$.
1. Red blood corpuscles. 2, 2. Platelets. 3. Small lymphocyte.

seen (fig. 78). Eosinophil cells are also found in the marrow, together with the basophil cells, and it is possible that the marrow is the origin of both, but the basophil are also found in connective tissue (fig. 27), and it seems more probable that they migrate from that position into the blood stream. There are numerous other classifications of the leucocytes of the blood, and three of them are here placed side by side with the one adopted above. It should be insisted that the systems of classification are unimportant compared with the recognition of the objects classified, and knowing what an author is talking

about. That is why the others are given here. They could be many times multiplied.

| | | | |
|---|---|---|---|
| *Polymorphonuclear Eosinophil* | *Polynuclear Eosinophil* | *Finely granular eosinophil* | *Polymorphocyte* |
| | | *Coarsely „ „* | *Granular Oxyphil* |
| *Lymphocytes small* | *Mononuclear small* | *Hyaline small* | *Microcyte* (Microlymphocyte) |
| *Lymphocytes large* | *Mononuclear large* | *Hyaline large* | *Macrocyte* (Macrolymphocyte) |
| — | — | (*Finely granular basophil*) | — |
| *Basophil* | *Basophil* | *Coarsely granular basophil* | *Granular basophil* |

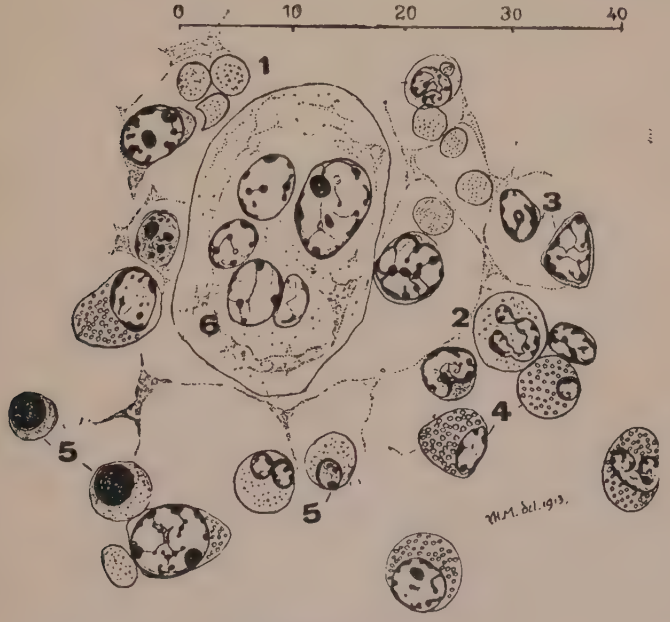



FIG. 78.—Red marrow. $\frac{1}{12}$″ × 4. L.

1. Red blood corpuscles (erythrocytes). 2. Polymorphonuclear leucocytes. 3. Lymphocytes. 4. Eosinophil corpuscles. 5. Erythroblasts. 6. Megakaryocyte.

**Red Blood Corpuscles**—Red blood corpuscles form by far the greater portion of the cells found in the blood and give it its colour. There are in the adult man five million, and in the adult woman four and a half million, red blood corpuscles per cubic *millimetre*, i.e. they are fifty times as numerous as the white blood corpuscles. In mammals the red blood corpuscles have no nucleus, the cells are biscuit-shaped and

in man measure $7\mu$ across. In the deer, the red corpuscles are much smaller, and so present a much larger surface in comparison with their bulk. In such blood they look almost like dust.

Red blood corpuscles often form rouleaux, like a mass of piled coins. The protoplasm is tinged reddish yellow, the coloration being due to a pigment, hæmoglobin. This pigment, when washed out of the corpuscles by such agents as ether or chloroform, can be made to crystallize, and these crystals have been used in the past as diagnostic means of deciding whether the pigment was blood pigment or not.

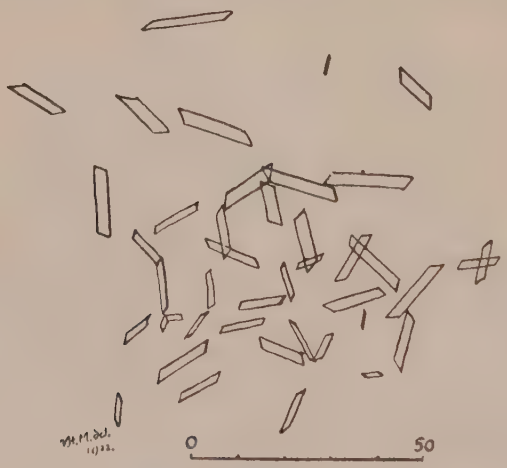



FIG. 79.—Hæmin Crystals. $\frac{1}{8}$" × 4. K.C.W.

Hæmin crystals, which are an acetic acid derivative of the pigment of the blood, can be prepared by heating blood, sodium chloride, and glacial acetic acid under a coverslip until boiling. They present a characteristic appearance (fig. 79).

In birds and reptiles and the lower vertebrates the red blood corpuscles are nucleated and oval (fig. 77): apparently in mammals it has been convenient to dispense with the nucleus.

The origin of red blood corpuscles is undoubtedly, in the adult, the red marrow of the ribs, the diploe of the skull, and the cancellous ends of the long bones. Here we find spherical nucleated cells which are tinged with hæmoglobin. The nuclei of these cells stain very darkly, and they may often be

seen showing mitotic figures. In fig. 78 several of these cells, called erythroblasts, are shown, one of them containing two nuclei (presumably immediately after mitosis has been completed). Whether these cells lose their nuclei, or whether they pinch off a part of their protoplasm which is then extruded into the blood, is a matter of debate. It is certainly true that when there is a need for a large production of red blood corpuscles (for instance, after a hæmorrhage or after the destruction of red blood corpuscles by arsenic or snake venom) there is great proliferation of the red marrow and active division of the erythroblasts. Sometimes nucleated red blood corpuscles are found in such conditions in the blood.

**Blood Platelets**—Another appearance which the student will meet with in shed blood is that of the platelets. Much discussion has taken place as to whether these are artefacts or not. Small masses of protoplasm one-third the size of red blood corpuscles are seen usually clumped together. They contain darker portions, staining with basic dyes which are perhaps nuclei, and they have amœboid processes which enable them to clump together. In frog's blood (fig. 77) they are more obvious, and are almost certainly not artefacts. They form centres from which coagulation of blood proceeds, and it has been thought that they are the origin of the clotting ferment.

**Marrow**—As so many of the cells of the blood have been mentioned as having counterparts in the marrow, it is convenient to consider that tissue here. Marrow is either white or red. White marrow is found in the shafts of the long bones and is white, owing to the predominance of fat cells. The fat cells are supported by a special and delicate variety of connective tissue, called reticular or reteform tissue (see fig. 32), and in the interstices are cells, such as we found in ossifying cartilage, osteoclasts and osteoblasts, together with other leucocytic cells. The red marrow is similar in composition. There is less fat (but even there it is in such amount that the clear spaces left, when the fat has been washed away in the ordinary treatment of the fixing, staining and mounting, may lead the unwary student to think of the thyroid gland—fig. 146), and there are many of the elements found in the blood, particularly red blood corpuscles.

Thus we see (fig. 78): (1) polymorphonuclear leucocytes with the nucleus perhaps less definitely lobed than in blood;

(2) numerous eosinophil cells, with a spherical rather than a horseshoe-shaped nucleus; (3) small lymphocytes; (4) basophil cells. In addition to these, we see (5) cells (myelocytes—marrow cells) with coarse granules, that stain with either eosin or methylene blue; (6) hyaline nucleated cells, staining brilliantly with eosin—erythroblasts—and containing hæmoglobin; (7) red blood corpuscles, the protoplasm of which stains similarly, and finally (8) large cells, many times the size of the others, called megakaryocytes, which have a large, many-lobed nucleus, with no apparent connection between the lobes. How these cells arise, and what is their function, is still obscure. They are usually found where red blood corpuscles are in process of development (fœtal liver and spleen). Apparently the only distinction between them and osteoclasts is that in the latter the nuclei are always separate; in the megakaryocytes there is usually an irregularly lobed, often annular, large nucleus, but sometimes there are discrete small nuclei. The distinction seems unimportant.

## CHAPTER III

## VASCULAR ORGANS

SO far we have been considering the elementary structure of the body—the ultimate formed elements into which it can be sub-divided. For the rest of the book it is our task to discuss the component parts of the different organs of the body, and the arrangement of those parts which characterize the organs. For instance, we discuss which of the elementary tissues and which of the free cells enter into the composition of the spleen, the trachea or the liver. The subject ceases to be histology proper, and becomes organo-histology, the warp and woof of the organs of the body.

Entering into practically every organ of the body are the blood vessels, and it is therefore logical to discuss first under organo-histology the structure of the blood and lymph vessels : the vascular organs.

These comprise the heart, arteries, veins, capillaries and lymph channels. A close relation in all these organs will be seen between their histological structure and their function.

**Arteries**—The function of an artery is to present : (1) a frictionless channel for the blood, therefore its interior surface must be smooth ; (2) to expand suddenly, under an injection of blood into it by the heart, therefore it must be elastic ; (3) to accommodate easily to the volume of fluid passing through it, it must therefore have contractile tissue, i.e. muscle, in its sheath ; and (4) to be strong, so that the high pressure under which it works does not burst it. It must therefore have a strong sheath of white fibrous tissue, which, however, must be loose to allow for the expansion, but strong enough to set a limit to that expansion. The histological structure of the artery shows adaptation to all these needs.

The artery under the low power will be seen to consist of three coats (fig. 80), called tunica intima, tunica media, and tunica adventitia. These names are usually abbreviated to

intima, which means innermost, media (middle), and adventitia, or externa (external).

Practically the elastic layer only of the intima will be

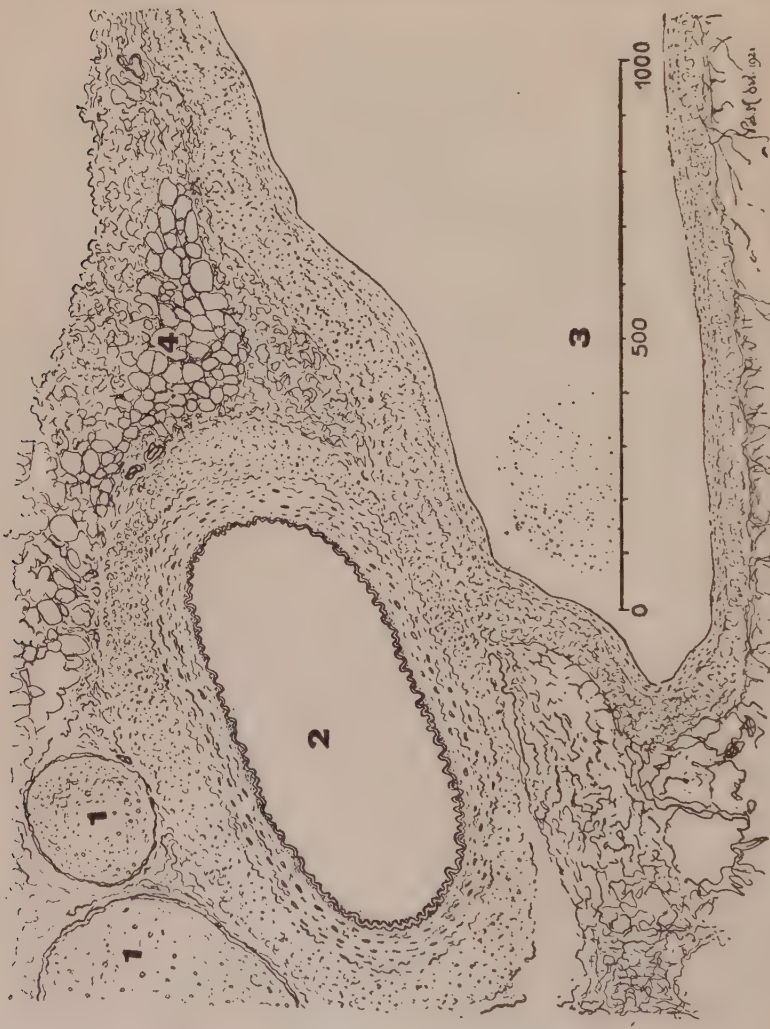



FIG. 80.—Artery, vein and nerves in connective tissue. $\frac{1}{2}$" × 1. G.A.H.
1, 1. Nerve bundles. 2. Artery. 3. Part of vein. 4. Adipose tissue.

seen. This appears white and shining and crinkled, owing to the fact that the artery has contracted during fixation.

The media is seen to consist of muscle fibres circularly

arranged with some firm elastic tissue. This is usually the most striking, and thickest, coat of the artery.

The adventitia, or externa, consists of elastic fibres, together with white fibrous tissue, and more loosely put together towards the exterior, to connect it with the fibrous tissue in its vicinity.

Under the high power (fig. 81) the intima is seen to consist of three layers. Internally there is the endothelium, consisting

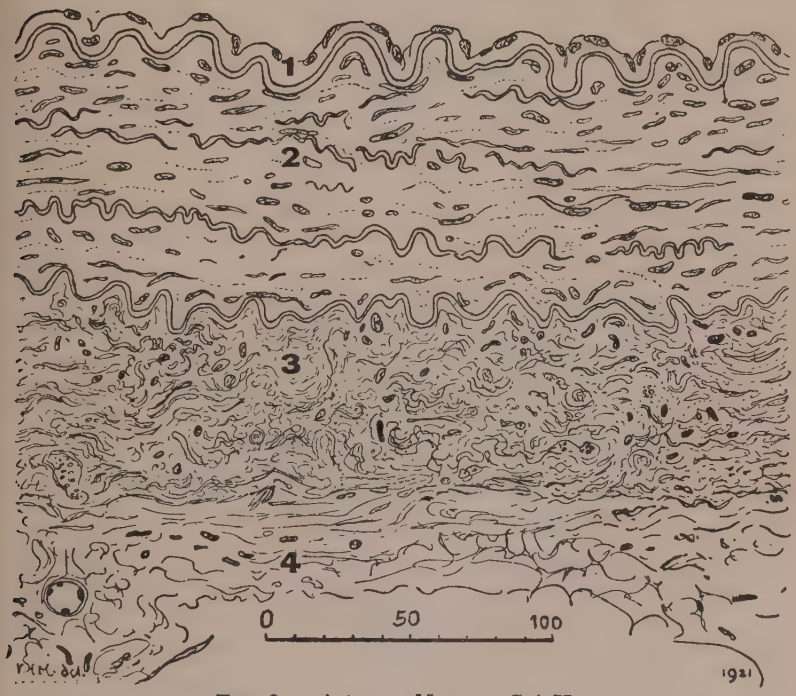



FIG. 81.—Artery. $\frac{1}{8}$″ × 2. G.A.H.

1. Tunica intima, consisting of endothelium, subendothelial tissue and elastic fenestrated membrane. 2. Tunica media, of muscle cells, connective tissue and elastic fibres. 3. Tunica adventitia, of connective tissue with much elastic material. 4. Connective tissue.

of flat, nucleated cells, forming a pavement epithelium over the whole of the inner surface. This coat gives the smoothness. The outlines of the cells are made visible by treatment with silver nitrate (fig. 121). Next, there is a layer of fine connective tissue, and then a layer of elastic tissue, which forms a membrane with openings in it, and for this reason is called the

fenestrated membrane. This elastic membrane marks the outer margin of the intima.

The media, which is a very thick coat in the smaller arteries, in the main consists of circularly arranged, unstriped muscle fibres; sometimes a few oblique fibres are present, and (rarely) some longitudinal. The outer layers are often broken up into bundles. There is a small amount of white fibrous tissue

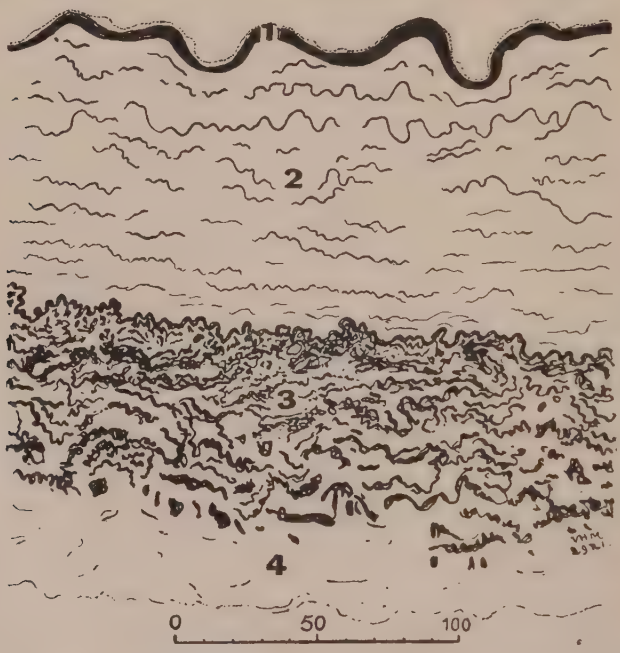
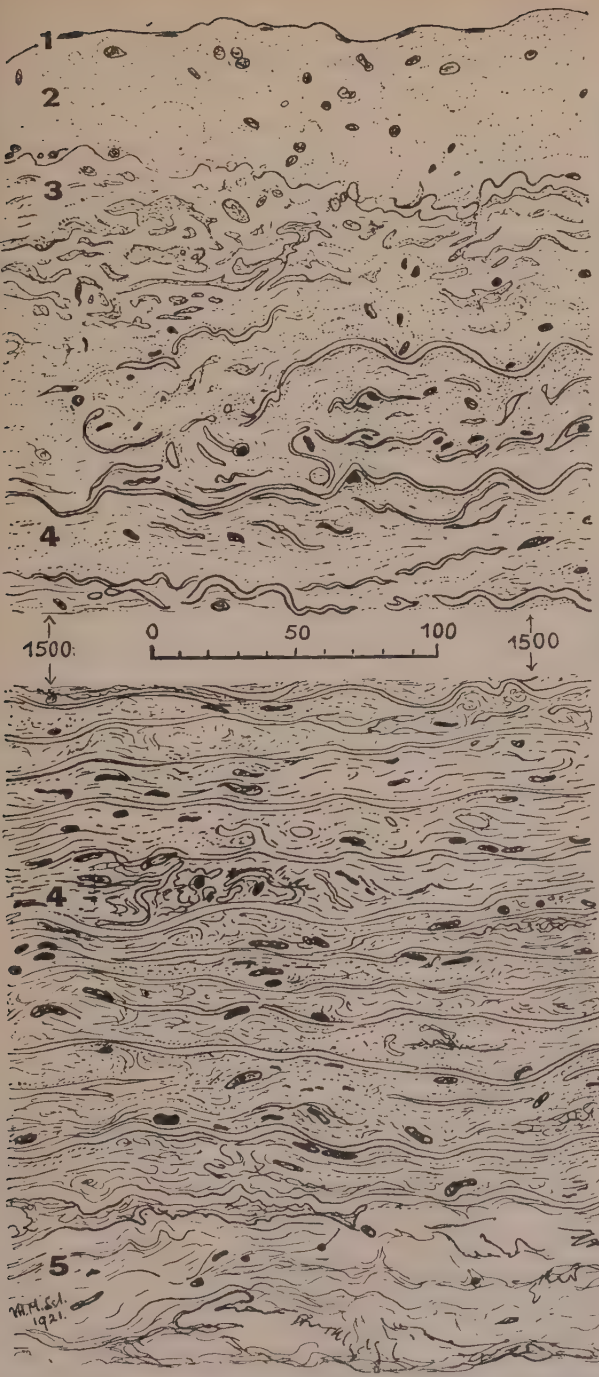



FIG. 82.—Artery. The same material as Fig. 81, but stained for elastic material. $\frac{1}{6}'' \times 2$. G.A.H.

1. Elastic fenestrated membrane. The endothelium and subendothelial layer are almost invisible. 2. Tunica media. 3. Tunica adventitia, showing much elastic tissue. 4. Adjacent connective tissue.

uniting the muscle fibres, and fine elastic fibres permeate the whole of this tissue, running both circularly and obliquely, and often toward the exterior, breaking the muscle fibres up into bundles.

The adventitia consists of heavy elastic fibres (often forming a fenestrated membrane on the interior), together with coarse white fibres, the amount of white fibrous tissue increasing as we pass towards the exterior. For elastic fibres, see fig. 82.




1. Endothelium.

2. Rest of tunica intima, which consists of white fibrous connective tissue and fine elastic tissue.

3. Dense elastic tissue of inner border of tunica media.

4. Middle and outer layers of media with much more regular arrangement of elastic fibres, muscle fibres and white fibrous tissue.

5. Adventitia.

FIG. 83.—Aorta. A large portion (1,500$\mu$) has been omitted from the middle of the tunica media. $\frac{1}{6}''$ × 2. G.A.H.

Modifications of these structures are to be seen in the large arteries. In the aorta we see: (1) in the intima more elastic tissue—even two elastic membranes—though nearer the heart the internal elastic membrane disappears as a membrane and is represented by elastic fibres only; (2) in the media, much more elastic material dividing this coat up into laminæ, the order being, elastic tissue, white fibrous tissue, unstriped muscle. This is repeated for each lamina, and we obtain 50–70 of such laminæ in the adult aorta; (3) in the adventitia are found longitudinal and circular elastic fibres, and externally looser and looser white fibrous tissue. (See figs. 83 and 84 and compare with figs. 81 and 82.)

Generalizing on the structure of arteries, we can say: (1) the proportion of elastic and white fibrous tissue in the middle coat is greater the less the artery has a contractile function. Therefore there is much more muscle and less white or elastic tissue in proportion in the small arteries which contract and dilate under the influence of the nervous system, and much more white and elastic tissue in the aorta, which is not contractile, though highly elastic; (2) where the arteries have much external protection and are unable to expand, e.g. in the cranial cavity, the muscle coats are thinner; and (3) where the pressure is low, the muscle coats (for instance, in the lungs) are thinner.

The relation of the intima to the media changes in proportion throughout life.

| | Intima. | Media. |
|---|---|---|
| New-born | 1 | 11 |
| Adolescent | 1 | 16 |
| Early middle age | 1 | 8 |
| Late middle age | 1 | 5·9 |
| Old age | 1 | 5·8 |

There is thus a hyperplasia (overgrowth) of the intima from adolescence on. The intima at middle age is three times as thick as at adolescence, and this development of the intima is due to an increase of the amount of elastic material, and is very marked in pathological cases of hardened arteries. It is possibly a reaction to increased blood pressure.

**Veins**—The structure of the veins is based on the same plan as that of the arteries. Quite frequently they will be seen running side by side with the arteries, and their distribution is the same (fig. 80). Microscopically, they are very much

FIG. 84.—Aorta. Stained to show elastic tissue. $\frac{3}{4}$" × 1. G.A.H.

1. Tunica intima with a little elastic tissue. 2. Tunica media of great thickness, with large amounts of elastic tissue. 3. Adventitia with some coarse elastic fibres.

larger in cross section, and their walls are thinner and are easily distorted by pressure.

With this macroscopic distinction there is under the microscope a noteworthy difference in the structure (fig. 85). The intima is thinner, very little more than an endothelium being visible. The media, so thick in the arteries, is here thin. There are a few layers of muscle tissue bound together by white fibrous tissue, and in its meshes there is a small amount of fine elastic fibres—much less than in the arteries. There is no elastic membrane on the inner surface of the tunica media. The tunica adventitia, which forms the bulk

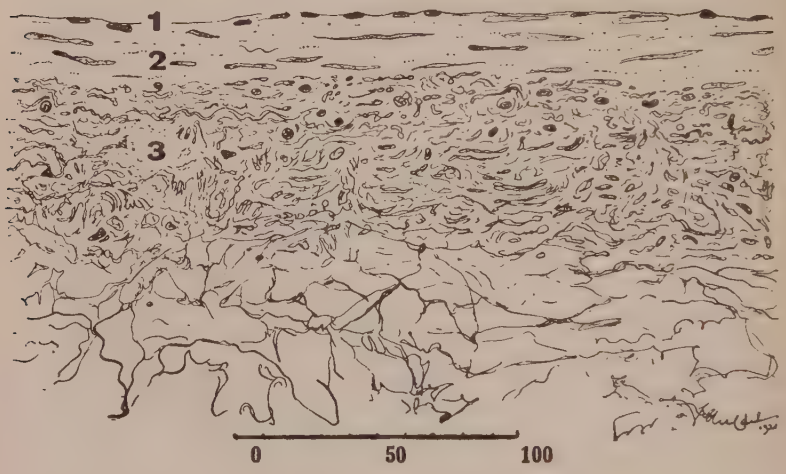



FIG. 85.—Vein. $\frac{1}{6}$" × 2.

The tunica intima is practically a line only, the nuclei of the endothelial cells projecting above the surface. The tunica media is very much reduced when compared with that of the artery. The tunica adventitia is much the same. (See Fig. 81.)
1. Tunica intima. 2. Tunica media. 3. Tunica adventitia.

of the walls of the veins, is practically as thick as in the arteries, and consists mostly of coarse fibrous tissues with coarse strands of elastic fibres running through it. But there is by no means such a development of elastic tissue as there is in the arteries (fig. 86). Summing up, the differences between the veins and arteries are:

(1) The veins have thinner walls with a greater lumen.
(2) There is much less muscle.
(3) There is much less elastic tissue.
(4) The adventitia is much greater in proportion to the thickness of the walls than in the arteries.

Each of these differences is linked up with the difference in function between the two structures.

**The Heart**—The heart wall consists of three parts : (1) an internal layer called the endocardium, which lines its cavities ; (2) a thick middle layer, consisting of muscle cells, called the myocardium ; and (3) an external layer, very like the serous covering of the other viscera, the pericardium (sometimes called epicardium).

The endocardium is lined with a pavement epithelium (endothelium) continuous with and similar to that of the veins and arteries. Next there is connective tissue with, in the deeper layers, elastic fibres. At times, plain muscle fibres

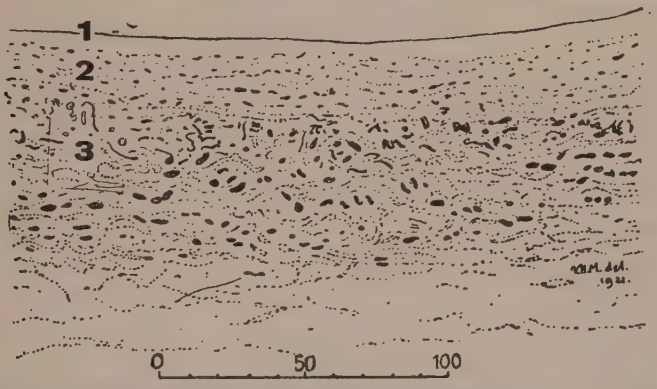



FIG. 86.—Vein, stained with orcein for elastic fibres. $\frac{1}{6}$" × 2. G.A.H.
Compare Fig. 82. There is much less elastic tissue in the vein than in the artery.
1. Tunica intima. 2. Tunica media. 3. Tunica adventitia.

may be found among the white and elastic fibres, and sometimes adipose tissue.

The myocardium is a thick layer of muscle cells upon which the functions of the heart depend. Cardiac muscle *cells* we have already described (p. 60). The direction of the muscle cells varies much, according to their depth and position. In the embryo heart it is possible to make out separate layers. It is certain that the bundles of fibres in the two auricles are continuous one with the other ; the same is true with the ventricles. Muscles which have origin in the left A.V. ring may pass over across the septum to the right ventricle, to be inserted into the chordæ tendineæ. But at first sight it appears that the muscle of the auricles is shut off from the

muscle of the ventricles by connective tissue. Closer investigation has shown, however, that a specialized muscle band, known as the bundle of His, consisting of cardiac muscle of rather embryonic type, connects the auricles with the ventricles. It has its origin in the A.V. node in the right auricle, passes downwards towards the ventricle, divides into two, and is supplied to the musculature of both ventricles.

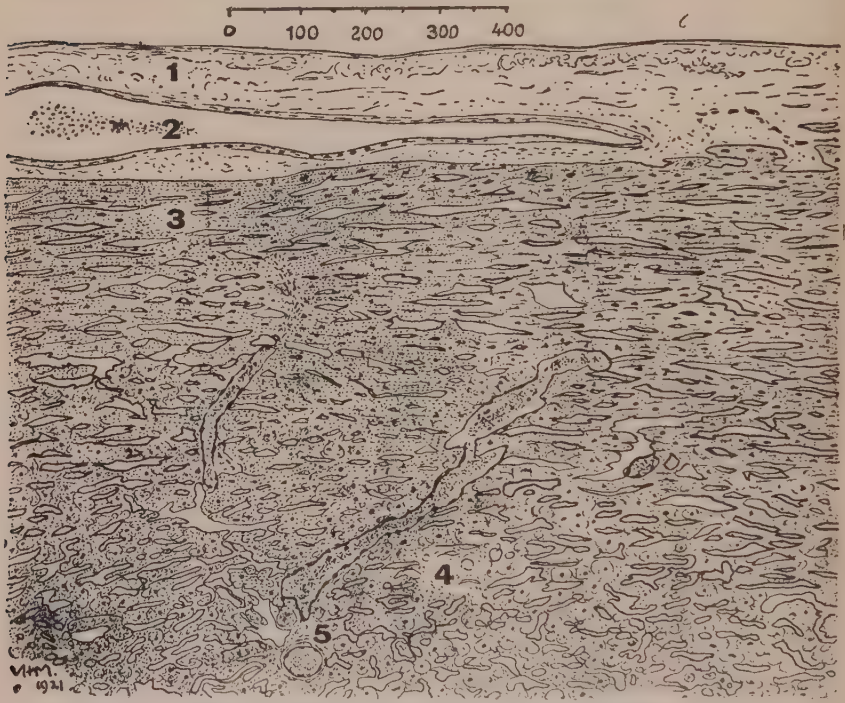



FIG. 87.—Wall of the Heart. ⅛″ × 2. G.A.H.

1. Pericardium. 2. Vein in pericardium. 3. Heart muscle (myocardium) cut parallel to the fibres. 4. Muscle fibres cut transversely. 5. Blood vessels within the myocardium.

Under the microscope the direction of the fibres can be made out partly by the direction of their nuclei and partly by the shapes of the spaces in between the muscle fibres. For instance, in fig. 87 the external fibres are running longitudinally, for the nuclei appear as oval rods, and the spaces between the muscle fibres are elongated lozenges. Deeper in the section the muscles are cut transversely, the nuclei now appear round, and the spaces between the muscle fibres are

very irregular. The student should familiarize himself with appearances of cardiac muscle, such as are shown in the two high-power drawings (figs. 55 and 56). In one the muscle fibres are shown cut longitudinally, and in the other transversely. Between the muscle fibres there is considerable space left. These spaces contain capillaries and lymphatics, but the whole of them is by no means filled with these two vascular structures.

Outside the myocardium we find the pericardium, which is often called the epicardium. Internally there is loose connective tissue, and a number of large blood vessels, fat cells, etc. This layer is sometimes called the tunica profunda. External to this is the tunica media, containing tendinous bundles of white fibrous tissue, together with elastic fibres, and on the outside of this the tunica externa, consisting internally of fine connective tissue, with a thin endothelial layer on the outside.

Joining the arteries with the veins is a system of multitudinous narrow channels, called capillaries. They can be looked on as consisting of nothing more than the thin walls of the endothelium of arteries or veins. Muscle and connective tissue have entirely disappeared from their coats. In longitudinal section they appear simply as narrow tubes, often of less calibre than the red blood corpuscle, with here and there a nucleus in the wall. In cross section capillaries are difficult to see, unless the section happens to go through the nucleus of the cell wall. Then something like a signet ring is seen, the stone of the ring being represented by the nucleus. Examples of these appearances will be seen in a large number of the diagrams in this textbook, notably figs. 51, 52, 55, 56. The junctions of the cells of the capillary walls with each other are demonstrable by silver nitrate, and are shown in the drawing of Bowman's capsule (fig. 121).

## CHAPTER IV

## GLANDS

THIS term is a good example of the inextricable mingling of macroscopical and microscopical terms which has occurred in histology.

Throughout the body are found structures easily separable from their surroundings, and shaped something like an acorn. The term gland is derived from the Latin glandula, which means a little acorn. Some of these glands have a peculiar structure, with the cells arranged in many little groups, each around a central lumen. Elsewhere we find, for instance in the mucous membrane of the stomach and the small and large intestine, a similar arrangement of cells around a lumen, and though no one could compare these structures with the shape of an acorn, their function is exactly the same as that of the cells in the first instanced structures. Consequently we now speak of the glands of the stomach and intestines without giving any broad macroscopic meaning to the term.

Glands can be broadly divided into the following two morphological groups:

(1) Glands possessing lumina or ducts opening (*a*) into a hollow organ, e.g. mucous glands of the nose and trachea, œsophageal, gastric and pancreatic glands, the kidney, the ovary and testis; or, (*b*) on the exterior of the body, e.g. sweat, sebaceous and mammary glands.

(2) Glands possessing no obvious ducts. Again, these can be divided into: (*a*) glands in which the obvious structures are fixed cells, for instance pituitary, thyroid and suprarenal glands; and (*b*) glands in which the free cellular elements are a marked feature, for instance lymph glands, spleen and thymus.

## GLANDS OPENING INTO THE ALIMENTARY TRACT

The simplest of the glands consists of a number of cells arranged around a central tube, the whole forming a cylinder, and constituting an alveolus (fig. 88). The nearest approach to simple glands is in the large intestine and the pyloric end of the stomach.

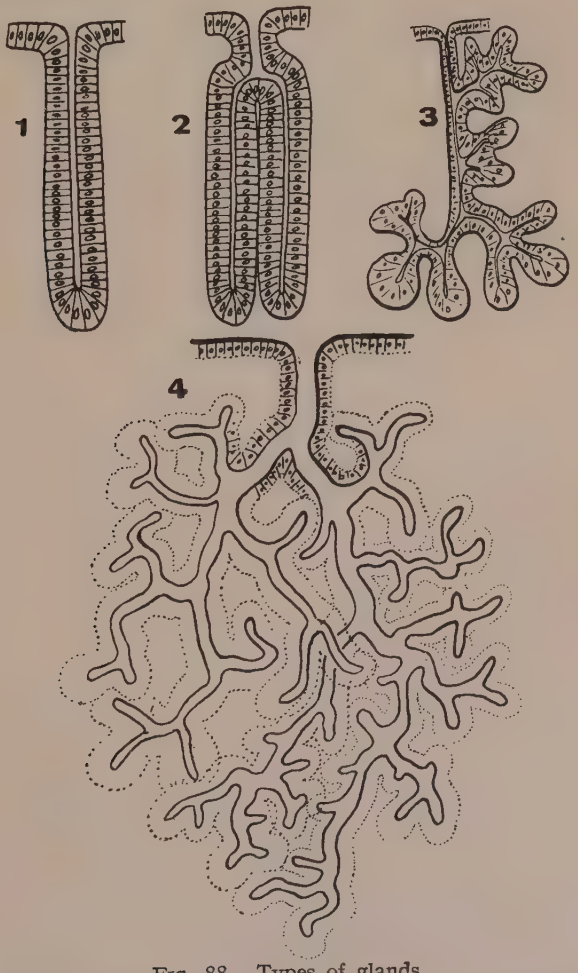



FIG. 88.—Types of glands.

1. Simple tubular. 2. Tubular with two branches. 3. Tubulo-racemose gland with one duct. 4. Complex tubulo-racemose gland.

Usually there is considerable branching of the alveoli, and the gland is then termed racemose (fig. 88).

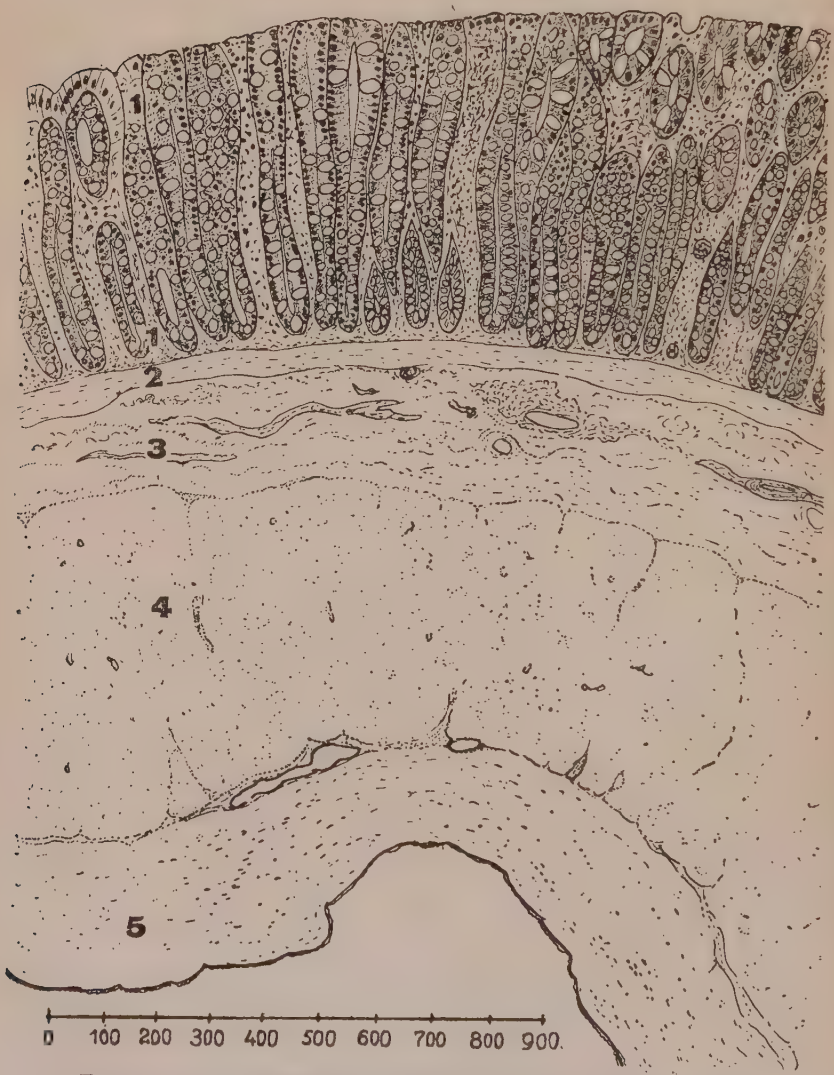



FIG. 89.—Large intestine (longitudinal section). $\frac{2}{3}$" × 1. G.A.H.

1. Mucous membrane with simple tubular glands containing many mucous cells (showing as clear oval areas). 2. Muscularis mucosæ. 3. Submucous coat with many blood vessels. 4. Circular muscle. 5. Longitudinal muscle coat.

## SIMPLE GLANDS

**The Glands of the Large Intestine** (figs. 89 and 90)—The glands here possess simple unbranched lumens, which

FIG. 90.—Portion of the mucous membrane of large intestine to show simple tubular glands. $\frac{1}{6}''$ × 1. G.A.H.

1, 1. Mouths of glands. 2, 2. Reticular tissue between the glands. 3, 3. Goblet or mucous cells. 4. Lower end of gland cut obliquely.

are often somewhat swollen at the lower end, and at the upper end open directly into the alimentary tract. They are lined with two types of cells, the one with small oval nuclei and faintly granular, well-staining protoplasm, the others (which are very numerous) are, in the ordinary laboratory

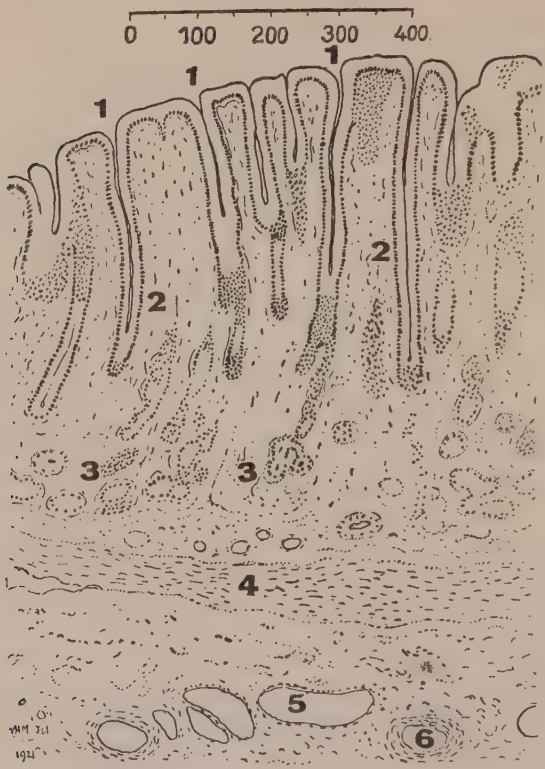



FIG. 91.—Simple tubular glands from the pyloric end of the stomach. $\frac{3}{4}$″ × 2. G.A.H.

1, 1, 1. Mouths of the glands. 2, 2. Glands cut parallel to their direction. 3. Glands cut transversely. 4. Muscularis mucosæ. 5. Vein, and 6, artery in the submucous coat.

preparation, swollen and glassy, with the nucleus frequently distorted by the pressure in the cell (fig. 90). This swollen, glassy appearance is associated, wherever it occurs, with the production of mucous material (mucin). Its presence in the cells of the glands of the large intestine should enable

FIG. 92.—Glands from the pyloric end of the stomach. High-power view of section of Fig. 91. $\frac{1}{6}''$ × 1. G.A.H.

1, 1, 1. Mouths of glands. 2. Columnar cells of glandular epithelium cut obliquely. 3. Unstriped muscle fibres traceable backwards to the muscularis mucosæ. 4. Gland cut obliquely. 5. Gland branching into two.

FIG. 93.—High-power view of pyloric glands in transverse section. $\frac{1}{6}$" × 2. G.A.H.

Note the columnar cells and the large lumina of these glands, One of them, as the result of fixation, etc., has pulled away from the basement membrane.

FIG. 94.—Glands of the mucous membrane of the small intestine: crypts of Lieberkühn. $\frac{1}{3}$" × 4. W.M.C.

1, 1. Villi. 2, 2. Crypts of Lieberkühn, some simple and some branched. 3, 3. Glands cut obliquely or tangentially.

anyone to distinguish these glands at a glance. (See page 19 for description of mucous cells.)

**The Pyloric Glands** (figs. 91, 92, 93)—Here the glands are simple and tubular, but at the lower end there is con-

FIG. 95.—Tubular glands of the cardiac end of the stomach. $\frac{2}{3}$″ × 2. C.
1, 1, 1. Mouths of glands. 2. Gland cut tangentially. 3, 3. Gland cut parallel to the general direction. 4. Glands cut transversely. 5. Muscularis mucosæ. 6. Vein.

siderable coiling of the tubes. Sometimes, however, there is a branching of the gland into two (fig. 92). The cells are, in contradistinction to those of the large intestine, of the crypts of Lieberkühn and of the cardiac end of the stomach, all of one type. They are columnar cells with an oval nucleus

situated near the base. It is rare in a section that the razor cuts one of these glands throughout its length along the lumen, with the result that the gland is cut tangentially through the nuclei or obliquely, giving rise to the appearances seen in

FIG. 96.—Tubular glands from the cardiac end of stomach. $\frac{1}{8}$" × 2. (Same preparation as in 95.) C.

1. Gland cut parallel to its general direction, showing two types of cells. 2. Parietal or oxyntic cells. 3. Chief, central or peptic cells.

figs. 91 and 92. In transverse section these glands appear as in fig. 93.

**The Crypts of Lieberkühn**—Here again the glands are sometimes simple and tubular, but more often there is a branching of the alveolus into two, three or four branches (fig. 94). As in the pyloric end of the stomach, the cells are columnar with small oval nuclei at their base, and, here and there, mucous cells can be made out.

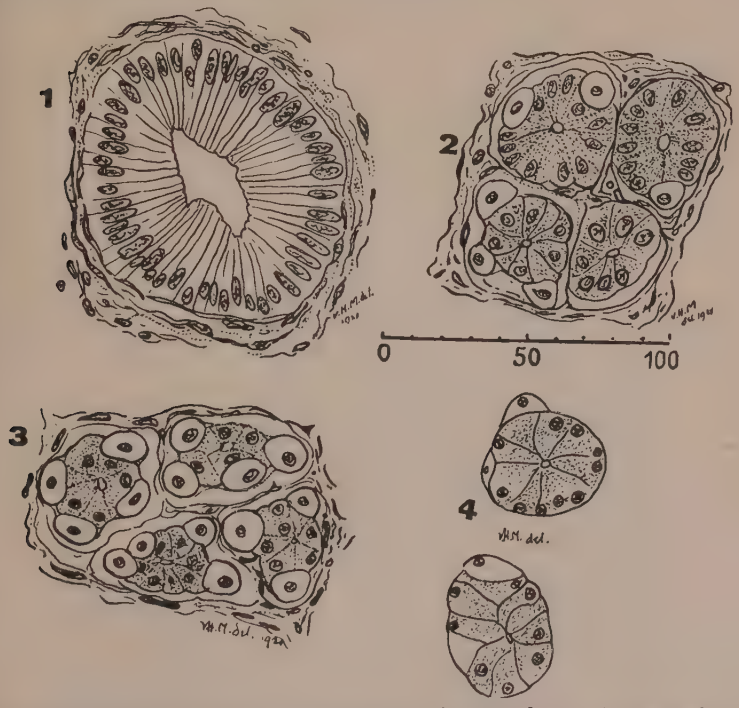



FIG. 97.—Tubular glands of cardiac end of stomach cut transversely at various levels. $\frac{1}{8}'' \times 2$. C.

1. At the mouth. The cells are columnar and the lumen is large. 2. Roughly one-quarter of the way down. As is shown by the connective tissue there are four branches to this gland. The lumen is now small, the chief, central or peptic cells are wedge-shaped and deeply stained, the ovoid, parietal or oxyntic cells are clear and shining. 3. Roughly half-way down. The ovoid cells are more numerous. 4. At the base of the glands near the muscularis mucosæ. The number of ovoid cells has decreased again.

**The Cardiac End of the Stomach** (figs. 95, 96, 97)—The glands here are closely comparable to those of the pyloric end of the stomach and the crypts of Lieberkühn in their general shape. They are rarely absolutely simple, but are

usually branched, having two, three or even four branches. At the mouths the cells are tall columnar cells, with oval nuclei, and the lumen is relatively large. This type of epithelium extends as far as the branching, approximately one-fourth or

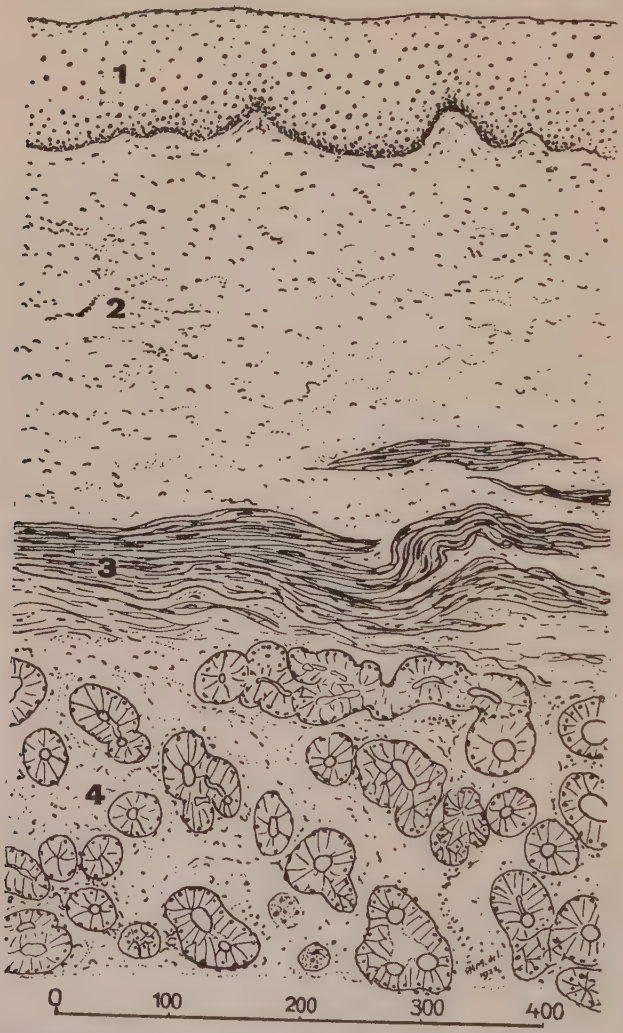



FIG. 98.—Œsophageal glands (longitudinal section). $\frac{2}{3}$″ × 4. W.M.C.

1. Stratified epithelium. 2. Connective tissue of mucous membrane. 3. Muscularis mucosæ. 4. Mucous glands of the œsophagus in submucous coat.

even from one-fifth down the length of the glands. Below that point the lumen narrows considerably, and the number of cells arranged round the lumen is smaller, moreover the cells are wedge-shaped in the main. There are two types of cell seen in the alveolus. The first, the chief, or central cells, predominate and abut on the lumen. They are wedge-shaped and have oval nuclei, and the cells are granular and stain well with dyes such as hæmatoxylin. On the outside of the alveoli are to be seen egg-shaped cells, with smaller, densely staining

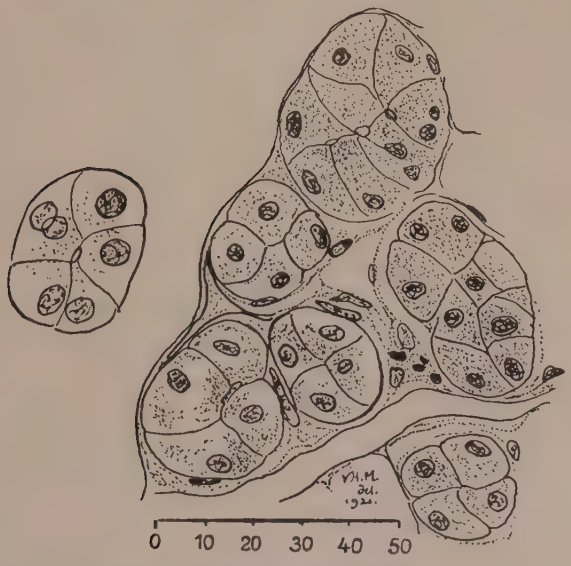



FIG. 99.—Serous salivary gland (parotid). $\frac{1}{8}$" × 4. C.

The alveoli consist of a few cells arranged around a small lumen, the protoplasm of the cells is granular, and the nuclei are oval to spherical and show marked chromatin. The basement membrane is well developed.

nuclei and clear protoplasm, which takes up acid dyes such as eosin, picric acid or Biebrich scarlet. At first there are not many of these cells (fig. 97), lower down the number often increases, while at the ends of the glands the number decreases again. The peculiar appearance and staining properties of these cells mark them off from any other gland that the student is likely to see under the microscope. No mistake should ever be made concerning them.

In fig. 97, it is interesting to note how the arrangement of the connective tissue around the alveoli shows that every

mouth of a gland, in the part of the section from which the drawing was made, corresponded to four alveoli lower down, i.e. the gland branched into four.

**The Œsophageal Glands**—These are another type of simple glands opening into the alimentary tract. They are simple tubular or tubulo-racemose glands, in which the alveolus is lined with columnar cells, and there is a moderately

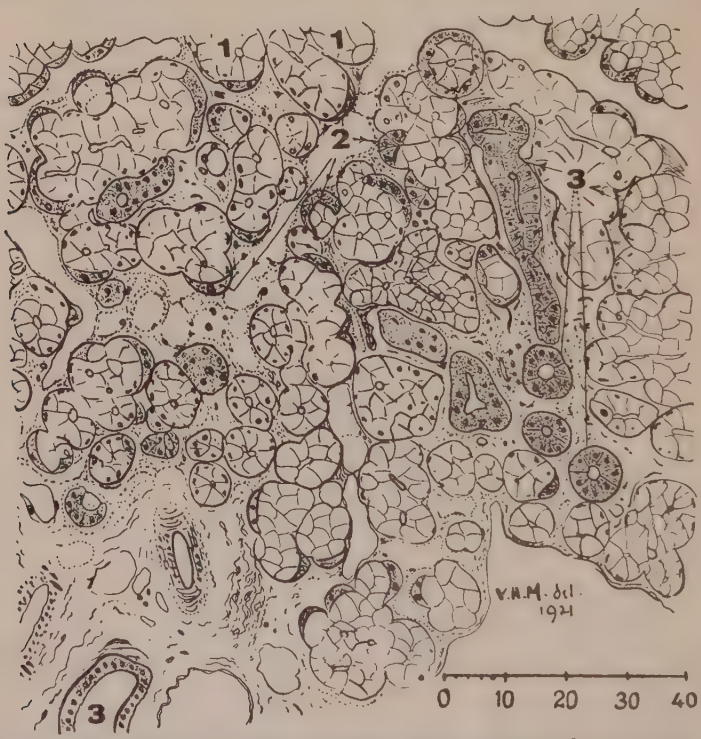



FIG. 100.—Mixed salivary gland showing mucous cells and every here and there a few serous cells. (Submaxillary gland.) $\frac{5}{8}''$ × 4. C.

1. Mucous alveoli. 2. Serous cells in the form of demilunes. 3. Ducts.

large lumen (fig. 98). These glands are situated in a somewhat unusual position for glands, that is, beneath the mucous coat.

The remaining glands whose ducts open into the alimentary canal are much more complex. They are the salivary glands, opening into the mouth, the pancreas and the liver, with their common duct opening into the duodenum.

## COMPOUND GLANDS

**Salivary Glands**—There are three main salivary glands, the parotid, the submaxillary, and the lingual. The parotid gland (fig. 99) in man has one type of cell only in its alveolus. Arranged round the lumen of the alveolus are from four to eight or more cells; they are wedge-shaped, and the protoplasm is granular, and the granules stain deeply with hæmotoxylin. This gives the cell a dark appearance. The nuclei are spherical, and about two-thirds of the length of the cell away from the lumen of the alveolus. Each alveolus is surrounded with a fine connective tissue membrane, with

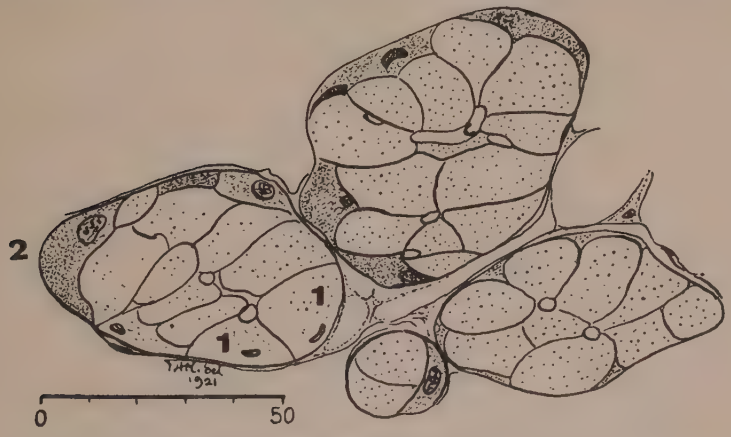



FIG. 101.—Mixed salivary gland (submaxillary). $\frac{1}{6}''$ × 4. C.

The alveoli show two types of cells. 1. Mucous cells, glassy in appearance, with the nuclei squashed flat. 2. Serous cells (demilune cells or crescents of Gianuzzi).

flattened oval nuclei in it, called the basement membrane, and these various alveoli are bound together by slightly coarser connective tissue. The lumina of the alveoli unite and empty into a duct, which is lined with cubical or columnar epithelium, and usually shows some striation of protoplasm. For the appearance of the ducts, see figs. 100 and 102 of mixed and mucous salivary glands respectively. The duct often stains more lightly than the serous cells. These ducts form a very conspicuous feature of all salivary glands, and should never fail to distinguish the parotid gland from the gland which most closely resembles it, the pancreas.

When we turn to the submaxillary gland (figs. 100 and 101) we find two types of cells, the one granular and darkly staining,

the other glassy in the ordinary preparation. The darker stained cell is undoubtedly a serous cell, comparable with those of the parotid, and the glassy cell, which has a flattened nucleus near the basement membrane, is a mucous cell,

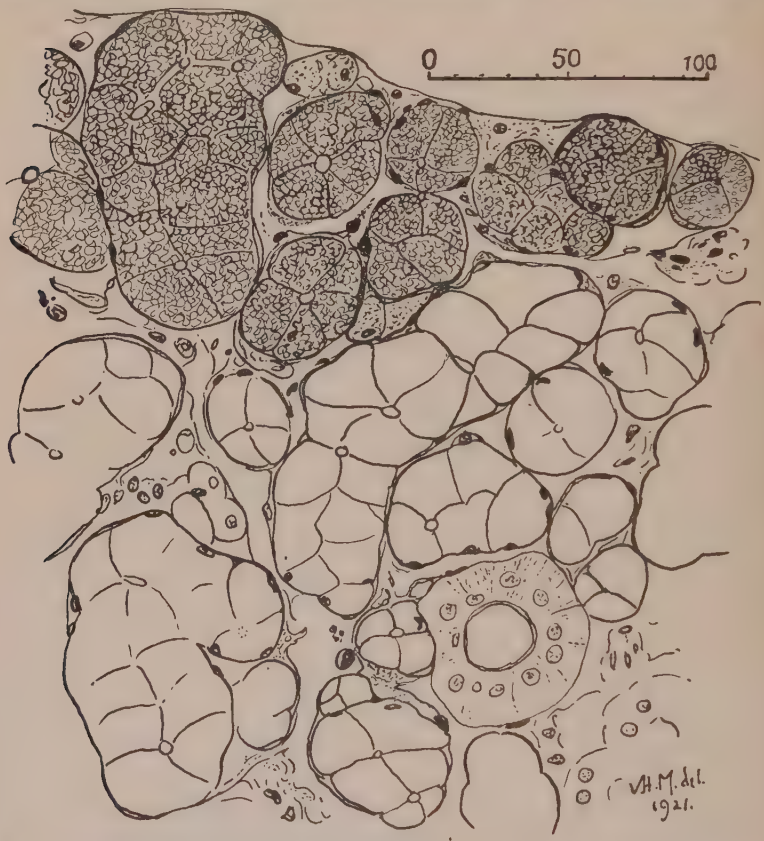



FIG. 102.—Mucous salivary gland (orbital gland of dog) in which the granules of mucigen have been preserved. $\frac{1}{6}$" × 2.

In the upper part of the section the granules have been indicated. In the lower they have been omitted, with the result that the drawing looks like that of a mucous gland fixed in the ordinary way.

similar to those found elsewhere in the glands of the alimentary tract, for example in the large intestine. If special precautions are taken to fix these cells in osmic acid vapour and then in their subsequent history never to allow them in alcohol of a less strength than 80 per cent., they are seen to be granular

and not glassy, and the granules stain strongly with methylene blue. On addition of water, the granules swell up and lose their power of staining and become glassy. See fig. 102, in which, in the upper part of the drawing, the granules have been indicated, and in the lower part of which they have been left undifferentiated, so that the lower portion of the drawing

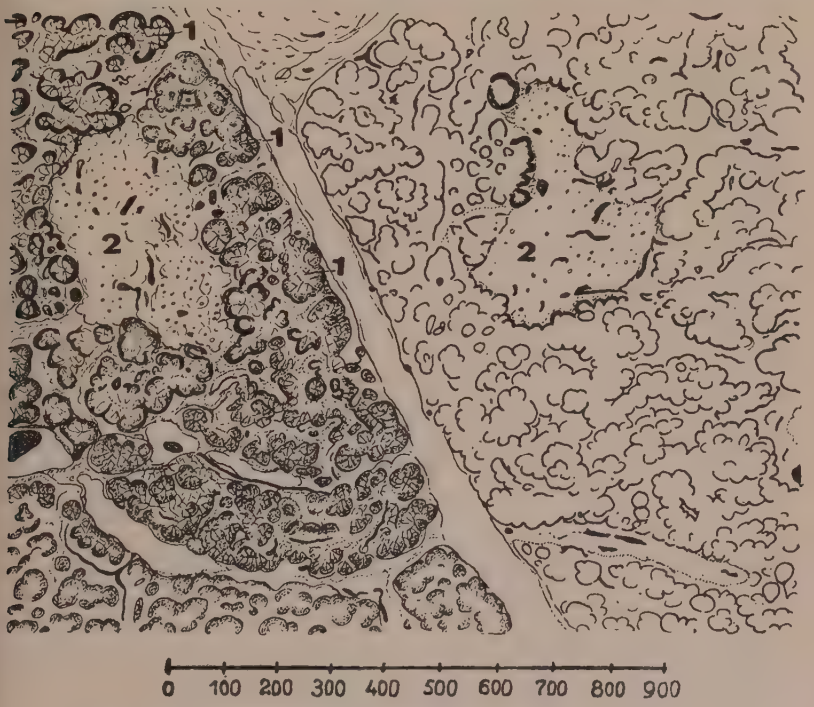



FIG. 103.—Pancreas, blood vessels injected. $\frac{3}{8}'' \times 1$. K.C.W.

The left half, only, of the drawing has been completed.

1, 1, 1. Alveoli showing a heavily stained outer zone. 2, 2. Islets of Langerhans (the cells of which are lightly stained), showing numerous blood vessels.

It will be noted that there are no ducts obvious in the whole of this section, which has an area at least four times that shown in Fig. 100.

appears much as if the gland from which it was made had been treated with the ordinary technique of watery fixatives and stains. Sometimes in the submaxillary gland we come across an alveolus either completely mucous or completely serous, but more usually they are mixed. Sometimes at the end of a mucous alveolus we have two or three serous cells. These by the swelling of the mucous cells are flattened into

a half-moon shape, and therefore are termed *demilune* or *crescent* cells, and have a highly characteristic appearance (figs. 100 and 101).

The sublingual gland in man is almost entirely mucous. There can be little doubt that the granules of the darkly

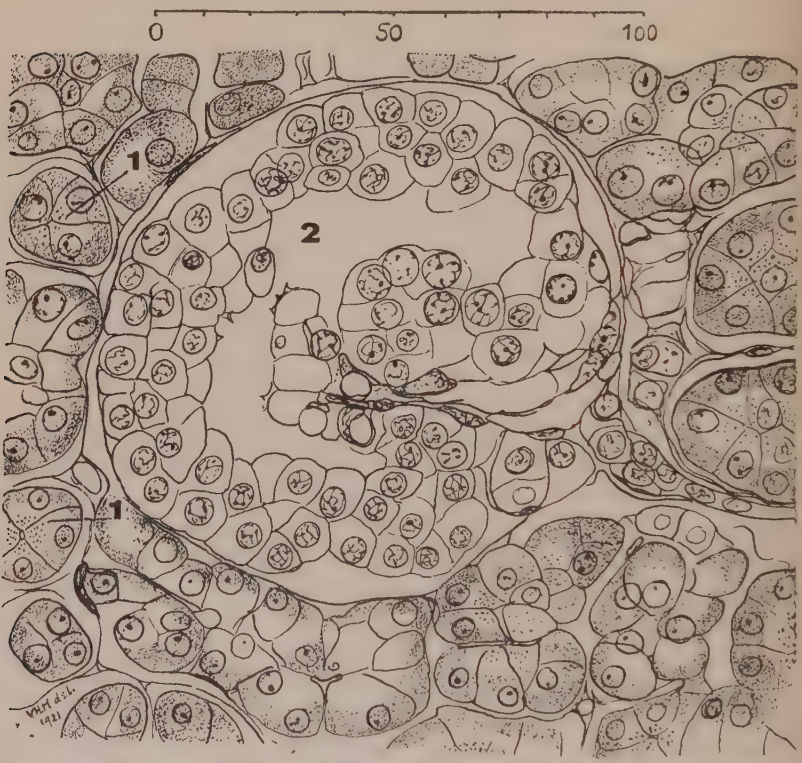



FIG. 104.—Pancreas of a child, showing ordinary alveoli and a small islet of Langerhans. $\frac{1}{8}'' \times 4$.

1. Typical alveolus, showing zonular staining, secretory granules around the lumen and nuclei with but little chromatin. 2. Islet tissue with small cells, large nuclei with a fine chromatin network, and faintly stained protoplasm.

stained cells of the salivary glands are the precursors of the secretion containing the ferment ptyalin, whereas the granules in the mucous cells are the precursors of the mucin. In confirmation of this we find that the parotid gland yields a watery secretion containing a starch-splitting ferment, while the

secretion from the submaxillary and sublingual is much more viscous and contains mucin.

**The Pancreas**—The pancreas, as stated above, closely resembles a serous salivary gland, but there are several distinguishing features. In the first place, the alveoli are not quite so distinct (see fig. 103); in the second, the protoplasm of the cells shows a marked differentiation into two zones; the outer (roughly one-third of the whole) stains darkly with hæmotoxylin, the inner zone, if it stains at all, stains with an acid dye, and contains granules (fig. 104). In addition, it is rare that we see a typical duct even in a low-power field (cp. the many ducts visible in the salivary glands), and lastly, we have islands of cells much more lightly stained, and having a large blood supply, known as the islets of Langerhans. These are a conspicuous figure in any low-power section (figs. 103 and 104).

On account of the twofold nature of the cells of the pancreas, namely, the ordinary alveoli and the islets, we should expect a double function in the pancreas. The serous cells are clearly the secreting cells, and supply the ferments of the pancreatic secretion. About the islets there has been considerable discussion. In addition to the secretory function of the pancreas, there is the function of controlling the carbohydrate metabolism of the whole animal. These islets have been assumed to be the seat of this function. In diabetes, in which there is a disturbance of the carbohydrate metabolism, these islets have been described as degenerating and, although this has been denied, it is generally held that an important part of the control of carbohydrate metabolism resides in these cells. They therefore belong to the group of glands with no obvious ducts, for the secretion is supposed to pass into the blood vessels found within the islets, and not into the alimentary tract. (See ductless glands.)

The one remaining important gland which secretes into the intestine is the liver.

**The Liver**—The liver, despite its size and unusual blood supply, has a comparatively simple histological structure. Anatomically the liver is a "gland," although from a derivational point of view it can scarcely be so termed. Its main constituent is "glandular" tissue, and it has an obvious secretory duct.

Every part of the liver has the same general structure,

although, naturally, where the blood vessels enter and leave the organ they are in excess. Over the whole, and sending down branches throughout the gland, is a connective tissue sheath, known as Glisson's capsule. The rest consists of glandular substance with a characteristic curious arrangement, and the vessels of an extraordinary (both in volume and kind) blood supply.

Under a low magnification the most obvious structures

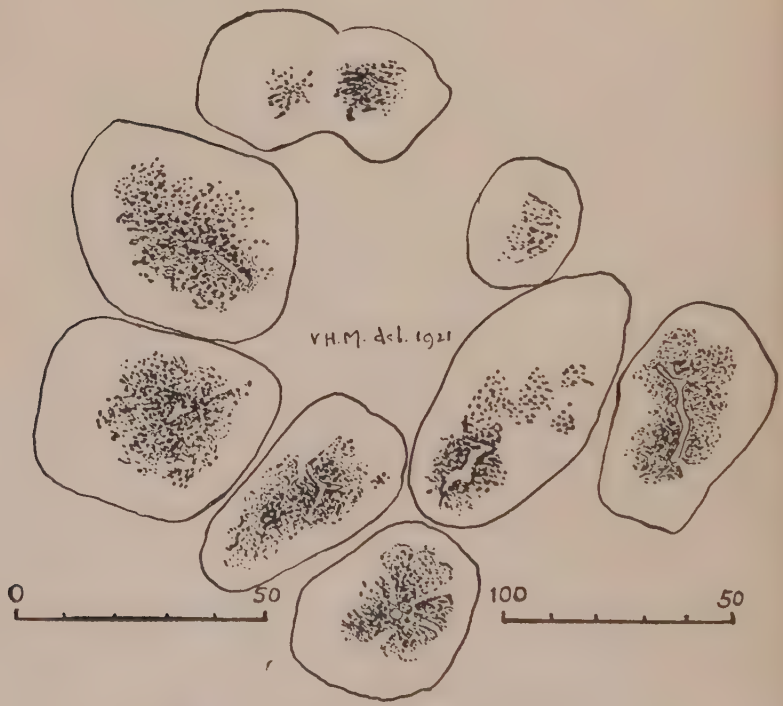



Fig. 105.—Secretory granules of pancreas.

in the liver are the lobules. These may be seen, even with the naked eye, mottling the surface. They consist, in typical cross section in mammalian liver, of a polygonal mass of cells, arranged radially round a central vessel (the intralobular vein, q.v., figs. 106 and 113). In longitudinal section the lobule has roughly parallel sides and a pyramidal end. In pig's liver the lobules are marked off from each other by

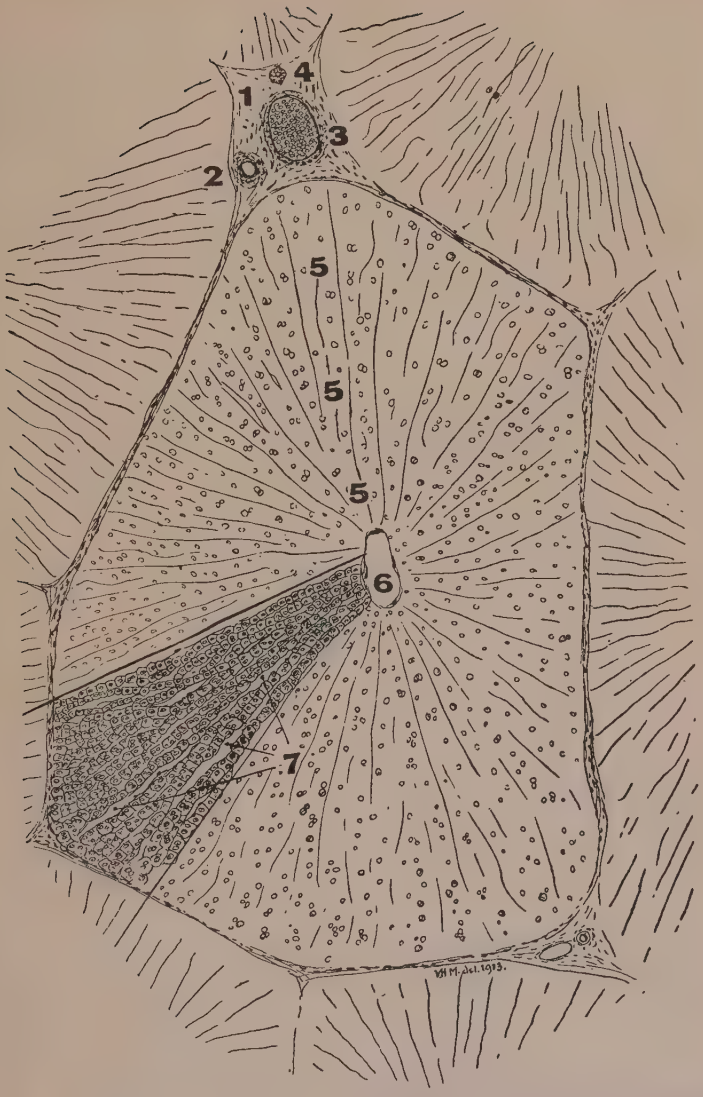



FIG. 106.—Liver, showing one complete lobule in transverse section and portions of several others. $\frac{2}{3}'' \times 2$. (The lobules are well marked off from each other in this preparation, because the liver is that of a pig.) One sector of the central lobule has been completed.

1. Connective tissue of Glisson's capsule, surrounding lobules and carrying blood vessels to and from the liver lobules. 2. Artery. 3. Vein (interlobular). 4. Bile duct. 5. Columns of cells arranged radially towards 6, the intralobular vein. 7. Sinusoid capillaries uniting the interlobular vein (i.e. branch of portal vein) with the intralobular vein (branch of the hepatic vein).

definite bands of connective tissue (Glisson's capsule), but in other mammalian livers the separation is incomplete. In this connective tissue, in one or other (or more) of the angles formed by adjacent lobules, run a group of vessels and ducts known as the portal canal. This consists of a large vein (a branch of the portal vein, called, from its position, the interlobular vein); a small artery (a branch of the hepatic artery); and a duct (the interlobular duct), lined with the cubical to columnar epithelium, typical of the duct of a secretory gland. The interlobular vein gives rise to capillaries,

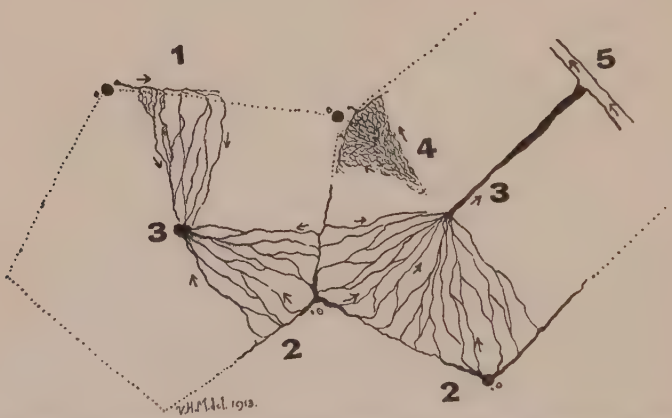



FIG. 107.—Diagram to show the direction of the flow of arterial blood, of portal (venous) blood and of bile in the liver. Two lobules are shown, one in transverse and the other in longitudinal section.

1. Arterial blood from the hepatic artery, supplying Glisson's capsule and then emptying into the intralobular capillaries. 2. Portal blood emptying into the intralobular capillaries and thence into, 3, the intralobular vein. 4. The bile capillaries. 5. The sublobular vein, whence the blood from both the hepatic artery and the portal vein pours into the hepatic vein.

which pass in between the columns of liver cells, and then *embouche* into the intralobular vein. The latter, at the base of the lobule, joins the sublobular vein, a branch of the hepatic vein (fig. 107). The course of the portal blood is: portal vein, interlobular vein, intralobular capillaries, intralobular vein, sublobular vein, and thence into the hepatic vein. The hepatic artery breaks up into capillaries partly supplying Glisson's capsule and partly turning in and joining the intralobular capillaries. The bile duct, the third member of the portal canal system, arises from the union of the bile capillaries which run in and out among the liver cells. They are

little more than lumina between the cells, though their walls are differentiated by appropriate stains from the cell cytoplasm. But the bile ducts into which they pour are lined with cubical epithelium. The interlobular bile ducts have columnar epithelium. The bile is passed in the portal canal in the opposite direction to the blood stream in the two blood vessels. Non-mammalian liver is built on similar but much looser lines.

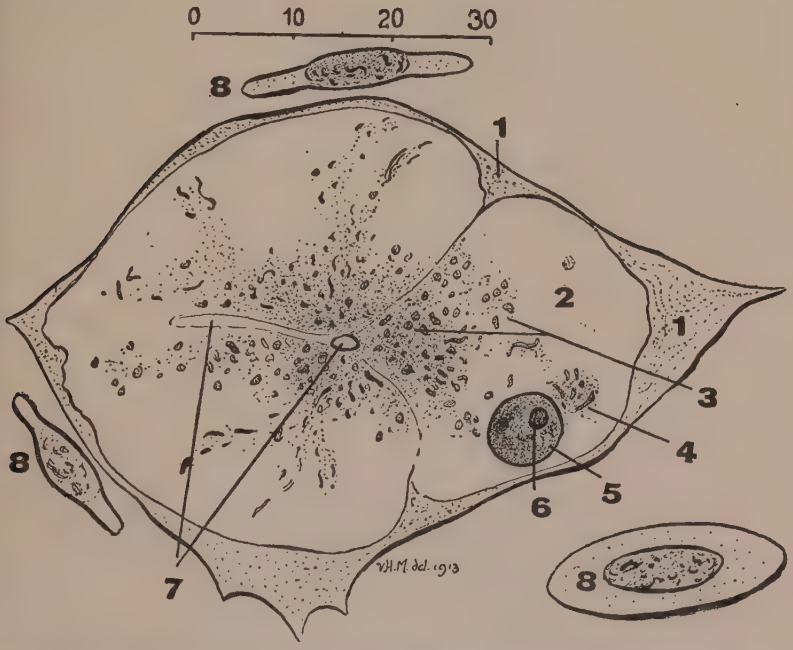



FIG. 108.—Alveolus of toad liver, cut obliquely, showing arrangement of the liver cells round the lumen of a bile capillary in amphibian liver.

1. Endothelium of blood capillaries. 2. Liver cell. 3. Granules (presumably secretory). 4. Chondriosomes or mitochondria. 5. Nucleus of liver cells. 6. Nucleolus. 7. Bile capillary. 8. Red blood corpuscles.

Once inside the liver lobule, the constituents are simply liver cells, blood and bile capillaries. For the blood comes into very close relation with the cells. There is nothing between it and them but the endotheliar lining of the capillaries. And the cells are arranged in rough columns, rarely more than two cells thick, and penetrating each cell there are canaliculi, tiny diverticula of the capillaries, bringing the blood

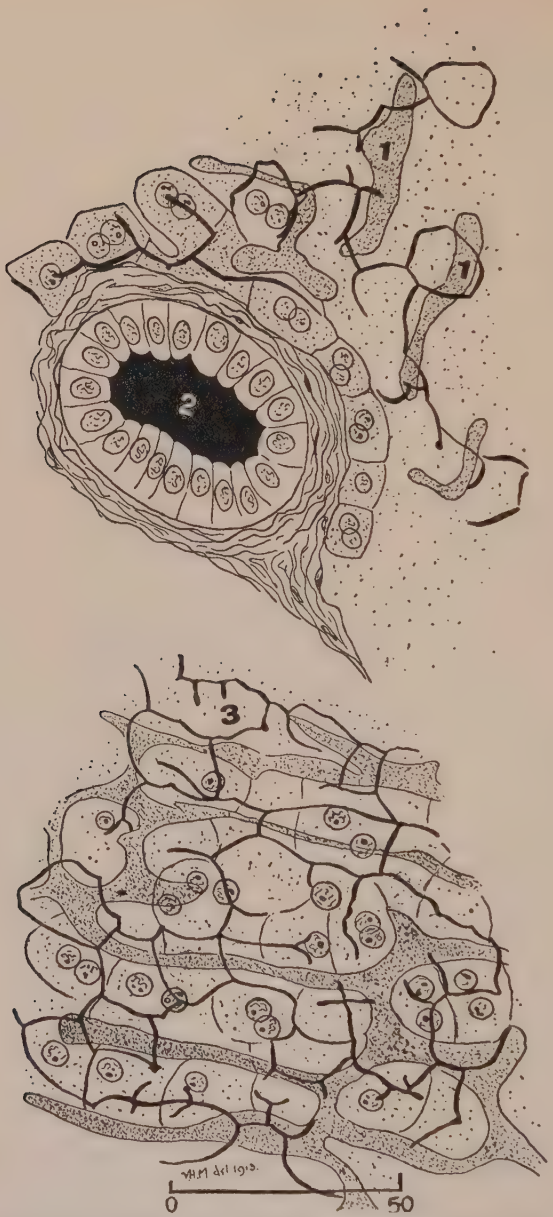



FIG. 109.—Liver of which the blood vessels and the bile capillaries have been injected. The bile duct and capillaries appear black and the blood vessels grey. From a section prepared by Hering. $\frac{1}{6}'' \times 4$. L.

1, 1. Blood vessel (intralobular capillary). 2. Bile duct. 3. Bile capillaries.

contents into the most intimate contact with the cytoplasm of the cells.

The arrangement of the cells in non-mammalian liver is typically "glandular" (in the physiological sense). The component cells are grouped into moderately long alveoli; in cross section three, four or five cells are seen arranged

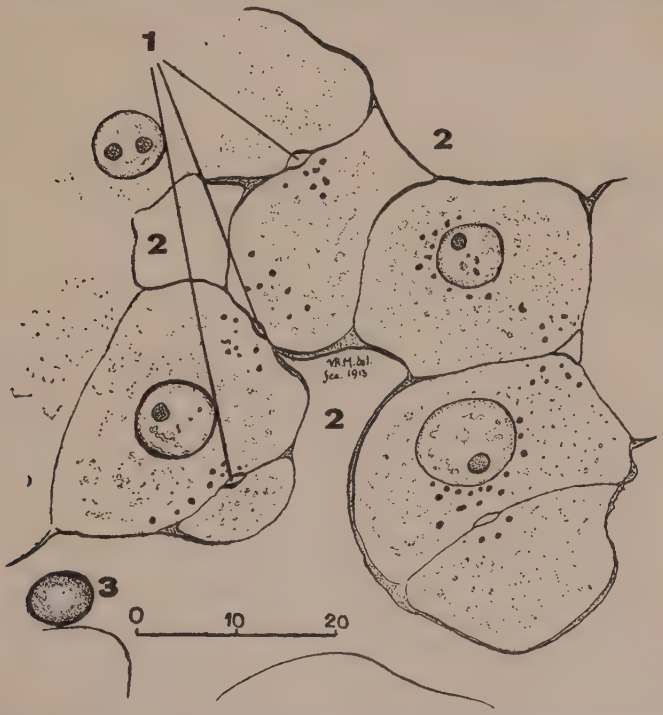



FIG. 110.—Mammalian liver showing iron-containing granules arranged around the cell nucleus or in the region of the bile capillary. $\frac{1}{12}'' \times 4$.

1. Bile capillaries with granules around them. 2. Intralobular capillaries. 3. Red blood corpuscle.

around a central lumen, the bile capillary (fig. 108). There is a central granular zone, suggesting that the granules are the precursors of the secretion, bile, and a peripheral zone of clear protoplasm in which the nuclei are found.

In mammalian liver the alveolar structure is there, but more difficult to make out, except in thin sections. The lumen—bile capillary—is not straight, but pursues a very erratic course in and out between the cells (figs. 109 and 111),

and the alveolus in cross section consists of two cells only (figs. 110 and 111). Moreover, to bear out the likeness to non-mammalian liver granules—iron-containing granules—are, in part, arranged round the lumen, just as in a typical secreting alveolus. But the acid-staining granules (*v. inf.*) show no zonular arrangement, and the morphological likeness to non-mammalian liver here breaks down.

The liver-cell in mammalia is cubical to polyhedral in shape; in the other vertebrates, wedge-shaped. Its size

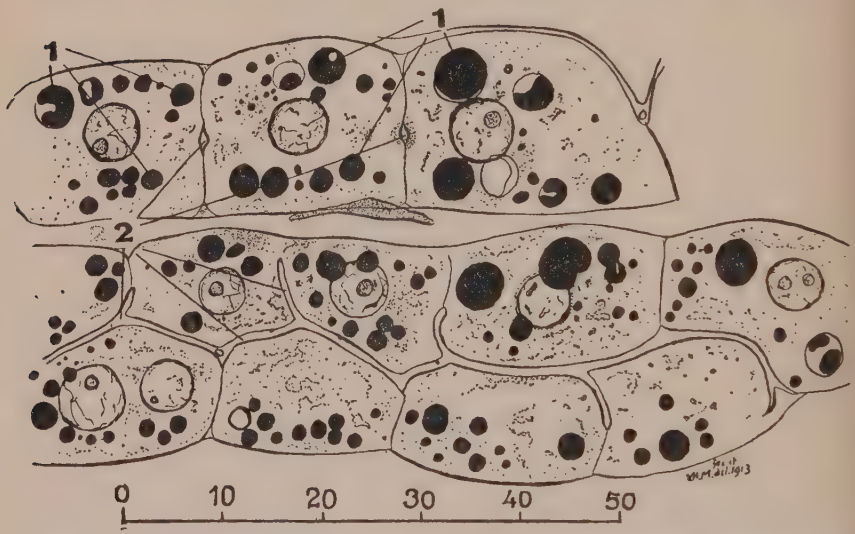



FIG. 111.—Liver cells infiltrated with fat. This occurs in hunger, pregnancy, lactation, diabetes, and in toxic conditions of the body. $\frac{1}{12}$" × 4.

1, 1. Fat globules. 2. Bile capillaries.

ranges from 10–30$\mu$, according to the state of nutrition of the animal and its species. There are usually two, sometimes three nuclei per cell, and unless the nucleus be crushed by some unusual substance (e.g. fat) in the cytoplasm, it is spherical. The chromatin forms a fine network on the exterior of the nucleus, and there are one, two, or three nucleoli (fig. 112).

The general mass of cytoplasm is, in fresh teased specimens, full of granules, which, on the disintegration of the cell, show Brownian movements. In fixed stained preparations the

cytoplasm may be hyaline, or display a network, or be highly granular, according to the fixative and staining reagents used. The granules are more easily preserved and stained in amphibian than in mammalian liver. They take "acid" stains (acid fuchsin, eosin, orange G.), as does, too, the nucleolus (fig. 108). Besides these acid-staining granules, there are other granules (black in unstained specimens; blue when treated with potassium ferrocyanide and hydrochloric acid), seen either in close relation to the nucleus or in the neighbourhood of the bile-capillary. These granules contain iron, and are the debris of red blood corpuscles (fig. 110). Further, frequently in normal livers, and especially so in the livers of hungry, pregnant, lactating or poisoned animals, globules of fat may be seen. At times, if the fat be abundant, they distort the shape of the nuclei of the cells (fig. 111). And last, among the cytoplastic contents, may be found clumps of glycogen. These are seen in animals well fed on starchy or sugary foods. The glycogen is usually present on the side of the cell towards the centre of the lobule (fig. 113).

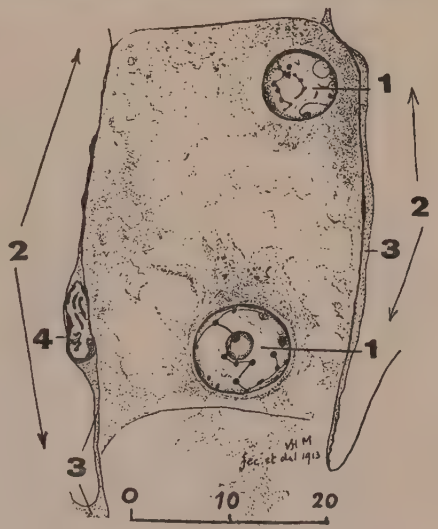



FIG. 112.—Liver cell. $\frac{1}{12}$" × 4.

1, 1. Nuclei, showing nucleolus and chromatin network. 2, 2. Intralobular capillaries. 3, 3. Endothelium of capillaries. 4. Nucleus of endothelial cell.

From the intimate relations that exist between the liver cell and the blood in that organ (a relation without parallel elsewhere in the body, though imitated in the suprarenal, thymus and other ductless glands) it would seem probable that the liver is concerned with the rapid addition to, or removal from, the blood of substances of metabolic importance. And the fact that the portal vein brings the chief blood supply to the liver suggests that these substances are largely the products of digestion in the alimentary system.

Histologically, both these surmises are confirmed by the increase of glycogen in the liver after a diet rich in carbohydrate ; by the increase of the size of the cell after a heavy protein diet ; by the appearance of fat in the cell when there is excessive fat metabolism in the body, and by the increase of iron-containing granules after hæmolysis.

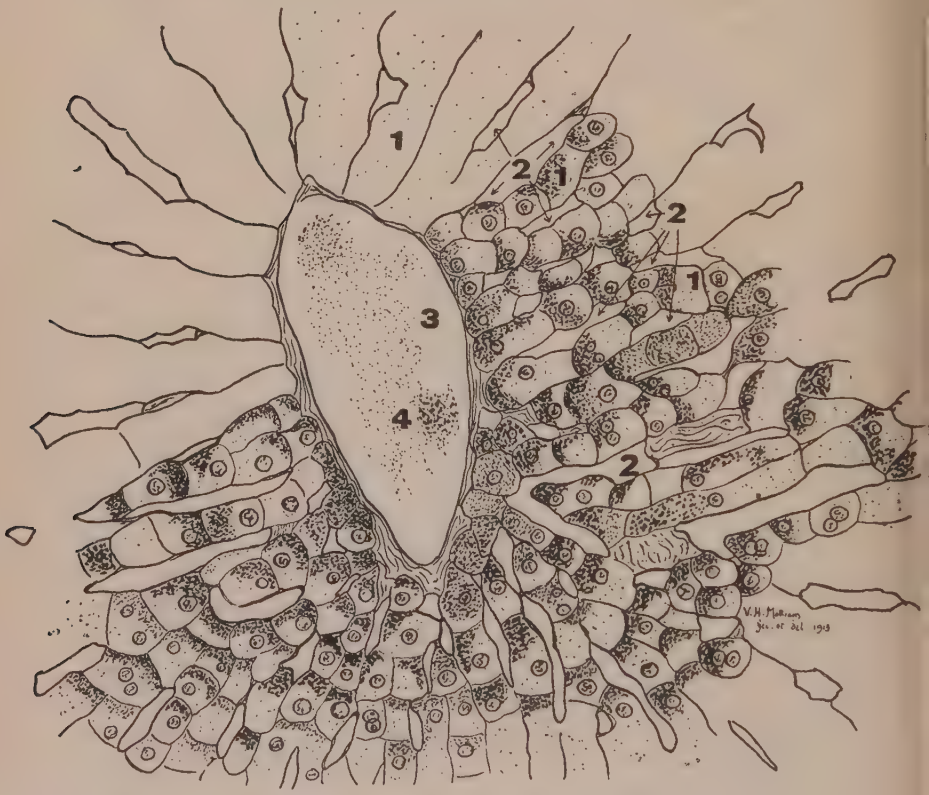



FIG. 113.—Part of a liver lobule showing glycogen. (The animal had previously had a diet rich in carbohydrates.) The glycogen stained with iodine. $\frac{1}{6}$" × 2.

1, 1. Trabeculæ of liver cells. 2, 2. Intralobular capillaries between them. 3. Intralobular vein showing debris of red blood corpuscles, and, 4, some glycogen. The dark granules in the liver cells, usually on the side towards the intralobular vein, are glycogen.

Further, the glandular structure of the liver (although profoundly modified in mammalia) suggests a secretory function, connected, among other things, with blood pigment

—see the relation of iron-containing granules to the bile capillaries. Other granules in amphibia, too, are in close proximity to the bile capillaries, though there is little morphological evidence for this in mammalian liver.

These suggestions, based on histology, are throughout confirmed by physiological and pathological evidence; for detailed results the reader is referred to works on those subjects.

## GLANDS WITH DUCTS OPENING INTO THE RESPIRATORY SYSTEM

**Mucous Glands**—Throughout the respiratory tracts there are simple and tubulo-racemose glands which secrete upon the surface of these tracts. Perhaps the best example can be found in the trachea (see fig. 114). These glands consist of a few branched alveoli in the submucous coat of the trachea. The alveoli have from small to larger lumina, according to their size and nearness to the final duct. The cells are wedge-shaped and tall—about 25$\mu$ high—and contain spherical, well-staining nuclei. The lumen of the duct, which is lined with cubical and columnar epithelium, varies in width, and is somewhat irregular in shape (fig. 114).

**The Lungs**—In addition, it is logical to include *lungs* under the classification of glands. In the fœtal animal the arrangement of the alveoli closely resembles that of a gland. In the mature animal there is a distinct modification of this appearance, but, nevertheless, we can consider the alveoli of the lungs as alveoli of glands lined with very flattened epithelium, and the bronchi and bronchioles can be considered to be the ducts of these glands.

The unit of structure in the lung is the lung lobule. This may be seen with the naked eye, marked off by fine septa of connective tissue extending down from the pleura, and forming a polygonal area on the surface. The structures inside such a lobule are: (1) the lobular artery; (2) the lobular vein; and (3) the system of alveoli or air cells, air sacs, atria, terminal bronchi, and respiratory bronchiole.

The respiratory bronchiole is an offshoot of a bronchiole or fine division of a bronchus. It is the duct of the lung lobule. It gives rise to three or more terminal bronchi or alveolar ducts, and each of these to several atria. From each atrium

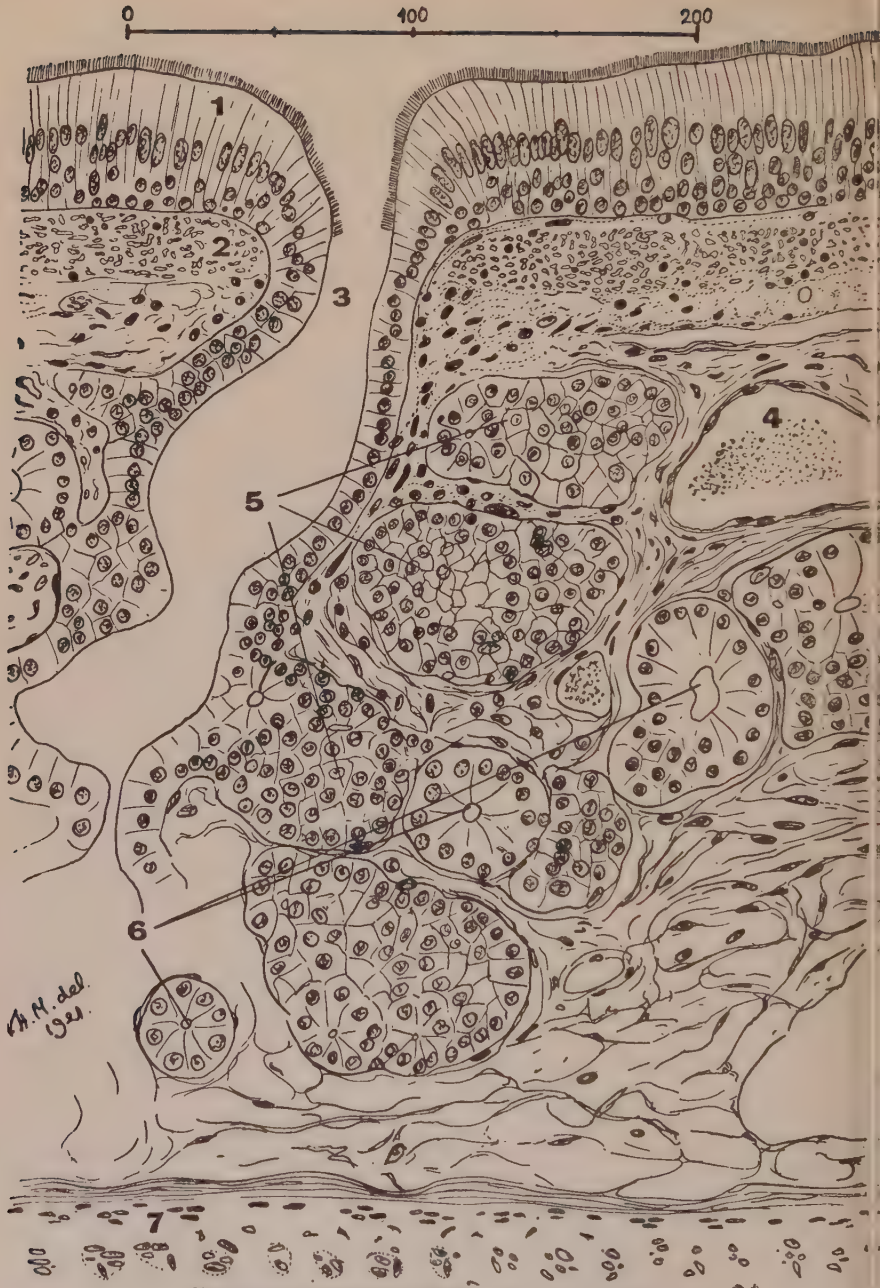



FIG. 114.—Tracheal glands. $\frac{1}{6}''$ × 2. G.A.H.

The section passes through the duct of a mucous tubulo-racemose gland in the tracheal wall. 1. Ciliated epithelium. 2. Elastic tissue. 3. Duct of gland. 4. Vein with debris of red blood corpuscles. 5. Alveoli of glands cut tangentially. 6. Alveoli cut transversely. 7. Cartilage.

arise air sacs, and in the walls of the air sacs are found the air cells or alveoli. The relations of these functional units to each other are shown in the diagram, fig. 117.

FIG. 115.—Lung (low power. $\frac{3}{8}'' \times 2$). G.A.H.

1. Small bronchiole. 2, 2. Arteries. 3. Vein. 4. Air sac or infundibulum. 5, 5. Air cells or alveoli.

Under the microscope the student must not expect to see anything so diagrammatic. He will note first of all structures

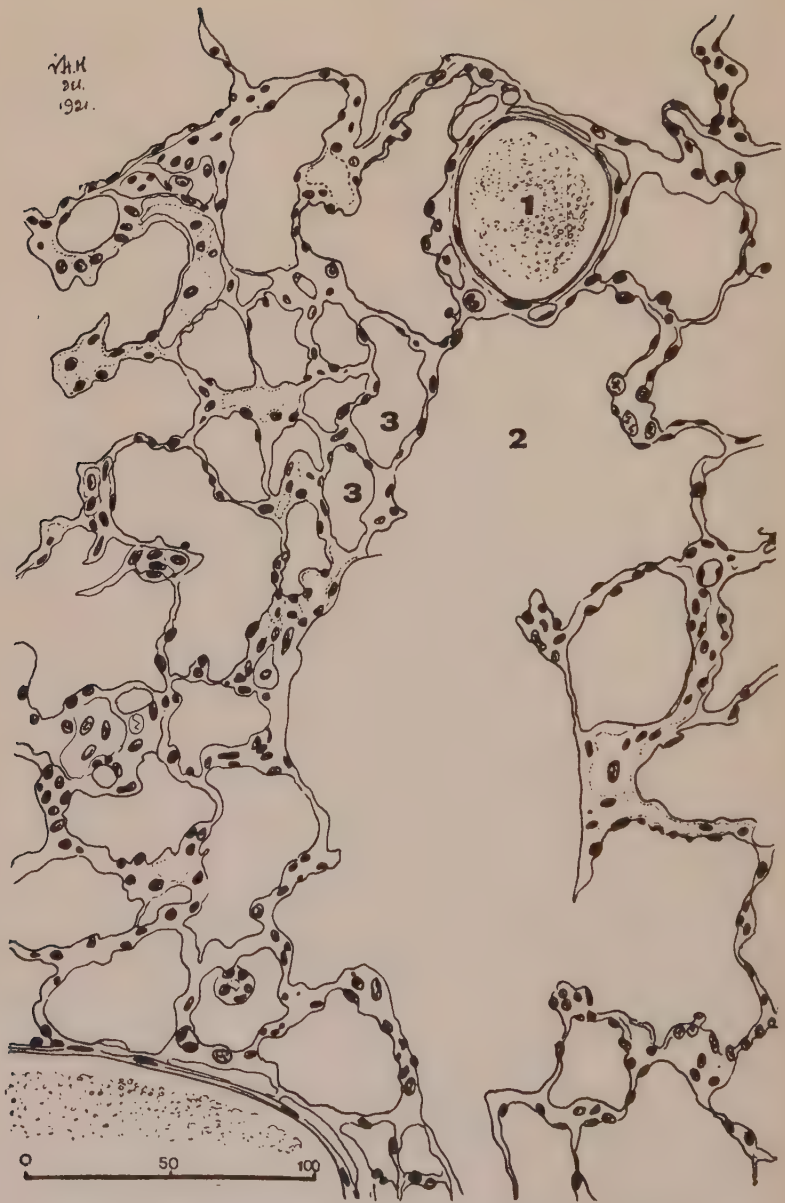



FIG. 116.—Lung (high power. $\frac{1}{6}'' \times 2$). G.A.H.
1. Vein with red corpuscle debris. 2. Air sac or infundibulum. 3, 3. Air cells or alveoli.

with a star-shaped lumen. These will have a band of unstriped muscle round them, and internally a ciliated epithelium, and under it much elastic tissue (see figs. 115 and 186). These

FIG. 117.—Diagram of the relation of alveoli to bronchioles, and the blood supply of a lung lobule (after Miller).

1. Bronchiole. 2. Terminal or lobular bronchiole. 3. Vestibule. 4. Atrium. 5. Infundibulum or air sac. 6. Alveolus or air cell. 7. Lobular artery. 8. Lobular vein.

are the bronchioles which are the branches of the bronchi. Their function is that of a duct and not of a respiratory

mechanism for the exchange of gases. Then he may note open spaces lined partly with ciliated epithelium and partly with thin squamous epithelium, and with a continuous muscle-fibre band around them. These are the respiratory bronchioles. He may also see similar spaces with flattened epithelium and an occasional muscle fibre. These are the terminal bronchi. More likely, neither of these structures will be identifiable, but the next important one will be an atrium (fig. 115). This is a large irregular space lined with flattened epithelium, and giving rise to similar but smaller spaces, the air sacs. In the walls of these are the smallest respiratory units, the air cells or alveoli.

The alveoli, which press closely against one another (fig. 116), have extremely thin walls, consisting of flattened endothelium-like cells. Running in between the adjacent walls of two alveoli are very numerous capillaries, so that the tissue interposed between the blood and the air is a minimum. In the walls of the alveoli are large amounts of elastic fibres, well seen on staining the lung for elastic fibres, and giving a picture almost identical with that of a lung stained by an ordinary method, so numerous are the elastic fibres.

Numerous arteries and veins are to be seen in any section of a lung. They accompany the ramifications of the bronchi to the lobules. The artery continues with the respiratory bronchioles and their ramifications, but the veins arise from the periphery of the lobule. The arteries of the lungs have less muscle fibre in their walls than arteries have elsewhere in the body, except in the cranial cavity.

## GLANDS WITH DUCTS OPENING INTO THE UROGENITAL TRACT

**The Kidney**—The kidney, which is essentially a gland to secrete urine, is composed of two parts, which are obvious to the naked eye, the cortex and medulla. Over the kidney there is a connective tissue capsule which, at the hilus of the gland, joins the ureters and dips into the medulla of the kidney and forms there the sinus. The cortex of the kidney is differentiated from the medulla by its colour (fig. 118). To the naked eye the cortex of the kidney is a brownish red, the interior being flesh-coloured. In some animals the medullary mass is shaped like a pyramid, with its base upon the inner aspect of the cortex, and the ureter opens out into

the chalice around the apex of this pyramid, but in animals such as man the medulla has about twelve pyramids, each one of which embouches into its own separate calyx, and each calyx into the pelvis of the ureter. The apex of the pyramid fits loosely into the cup of the calyx roughly as a ball into a socket, there being a space between the two filled by the

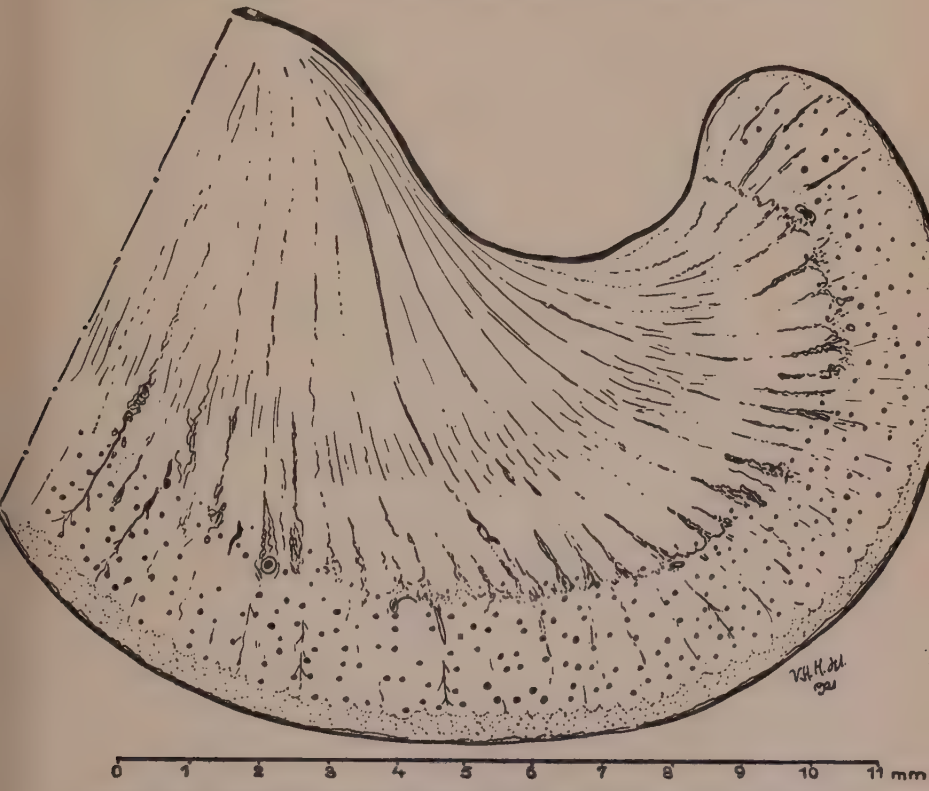



FIG. 118.—Hand lens view of a section of injected kidney, showing division into medulla and cortex, the medullary rays and the Malpighian bodies in the cortex.

secretion of the kidney. As was said before, the stem of the calyx is a branch of the ureter, which is the duct of the kidney.

The structure of the kidney can best be understood by following the blood supply. The renal artery branches follow the divisions of the ureter. The branches enter the substance of the kidney, and, dividing, form an incomplete series of

FIG. 119.—Diagram of blood flow through and urine flow in and from the kidney.

1. (At the left-hand bottom corner) Artery of incomplete arterial arch at junction of cortex and medulla. 2. Arteries to medulla. 3. Artery to cortex with nine branches. 4, 4. Malpighian bodies, consisting of, 5, glomerulus and, 6, Bowman's capsule. 7. Afferent vessel. 8. Efferent vessel breaking into, 9, capillaries around the tubules. 10. Convoluted tubules. 11. Descending tubules. 12. Loop of Henle. 13. Ascending tubules. 14. Second convoluted tubules. 15. Collecting tubules. 16. Duct of Bellini. (Plain arrows indicate direction of blood flow; double crossed arrows that of urine.)

arterial arches, in the neighbourhood of the junction of the medulla and cortex. At regular intervals each arch gives off branches, the radial arteries, which pass out at right angles into the medulla and cortex of the kidney (see figs. 118 and 119). In an injected specimen there can be seen with the naked eye at, and externally to, the region of this arch formation, a number of tiny bodies, first described by Malpighi from an uninjected specimen. These bodies, it can be seen with a hand lens, arise from the radial arteries, and indeed are a mass of capillaries closely rolled up into a ball, to which the name glomerulus has been given (figs. 118 and 120). Fig. 119 should make clear the course of the blood through these blood vessels. Each glomerulus has an afferent and an efferent vessel, and the afferent appears both larger and more muscular than the efferent (fig. 121). The efferent vessel then breaks up again into capillaries around the tubules of the gland, these reunite and form a vein which follows approximately the same distribution as the artery.

The secretory tubules of the kidney have their origin in a structure known as Bowman's capsule (fig. 121). This is a double hollow sphere of two layers of extremely thin epithelioid cells. Each Bowman's capsule grasps a glomerular tuft of blood vessels, much as, but more completely than, a hand will grasp a tennis ball. The outer wall of Bowman's capsule is practically spherical, the inner adheres to the head of the glomerular tuft (see fig. 121). Any fluid, then, that passes from the glomerular tufts into the hollow space of Bowman's capsule has to pass: (1) through the capillary walls in the tuft, and (2) through the inner surface of Bowman's capsule into the crescent moon-shaped space between the two walls of the capsule. From this moon-shaped space it passes out by an efferent tubule into the uriniferous tubules of the kidney. Fig. 121, which is a silver nitrate preparation made from the frog's kidney, should make this complicated arrangement clear. At the right-hand top corner we have the afferent artery to the glomerulus. The balloon-shaped large body is Bowman's capsule, the outer wall alone showing. Into this the afferent vessel passes and breaks up into a mass of capillaries, which, in the preparation under discussion, take up only one-third of the room inside the capsule. This is so, *because at the moment of fixation by the silver nitrate this kidney was secreting vigorously.* In a resting kidney the

FIG. 120.—Cortex of injected kidney. $\frac{1}{6}'' \times 1$. G.A.H.

1. Capsule of kidney. 2. Outer layer of cortex, consisting of convoluted tubules and blood vessels. The outlines of the tubules are shown by the dense capillary network around them. 3. Glomerular tufts (blood vessels). 4. Artery supplying several glomeruli. 5. Region of straight tubules (i.e. a medullary ray).

glomerulus fills the whole of Bowman's capsule. At the same right-hand top corner the efferent vessel is seen making its way from the capsule. It is smaller than the afferent vessel.

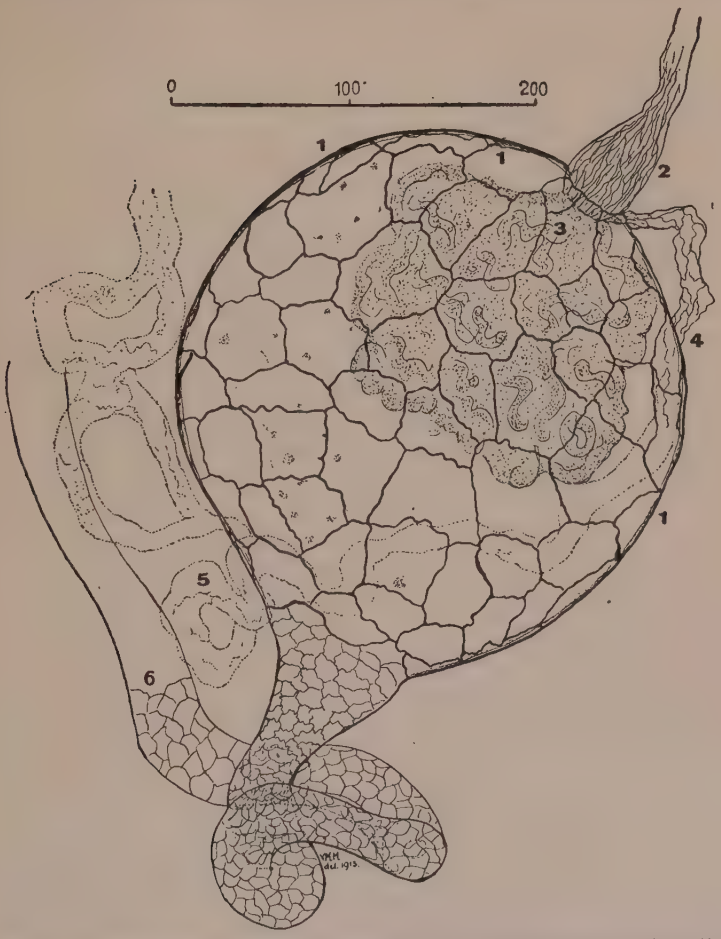



FIG. 121.—Bowman's capsule, glomerulus, etc. (frog), stained with silver nitrate.

1. Bowman's capsule. 2. Afferent artery. 3. Glomerulus. 4. Efferent artery passing down behind the capsule. 5. Capillaries arising from efferent artery forming a network around tubules other than the one shown. 6. Convoluted tubule in direct connection with Bowman's capsule.

It passes down behind the capsule to break up into capillaries round the uriniferous tubule arising from another Bowman's capsule, not its own. In the figure will be seen issuing from

the lower end of Bowman's capsule a funnel-shaped tubule which instantly begins to coil in all directions. It is a convoluted tubule.

The fluid from Bowman's capsule then passes through a convoluted tubule (see fig. 119). Then this tubule becomes straight and runs in a radial direction towards the medulla of the kidney. At first the tubule is wide, then it suddenly narrows, and then abruptly alters its direction and retraces its path, running radially away from the medulla. Then follows a second convolution of the tubule, and then the tubule empties itself into a collecting tubule, which passes radially towards the calyx of the ureter and receives, in its course, drainage from the other uriniferous tubules arranged on exactly the same plan.

The course of the urine is, then, from the Bowman's capsules into the convoluted tubules, then into the straight descending tubules, then the ascending tubules, then into the second convoluted tubules, and finally into the collecting tubules, which open into the wide ducts of Bellini, which in their turn open out on the surface of the medullary pyramid (see figs. 119 and 121, which should make this clear). But the actual appearance of the kidney in section is difficult to understand. In a section lengthwise through the kidney, we see that there are in the cortex alternate radial bands (fig. 118). The first are straight, and extend down from the cortex to the medulla. These are the medullary rays, and consist of the descending and ascending tubules, together with the collecting tubules. The second consists of Malpighian bodies, together with convoluted tubules. A series of tangential sections through the kidney will pass: (1) through the capsule; (2) a zone consisting of convoluted tubules only; (3) a zone containing convoluted tubules, Malpighian bodies and medullary rays; (4) arterial arches in addition to these; (5) a layer containing straight tubules and blood vessels, only with no more convoluted tubules or Malpighian bodies; (6) a layer where there are no more ascending or descending tubules, but simply collecting tubules and tubules of Bellini. The structures of the different tubules are as follows:

(1) THE CONVOLUTED TUBULES (see figs. 120 and 122). These are seen, as their name implies, to bend in all directions, and in any section of the cortex of the kidney they are seen cut in every plane. They bear a close resemblance to the

alveoli of secretory glands. Each consists of a number of cells, arranged in an alveolus with a large lumen[1] in the middle, standing upon a basement membrane. Each cell has a spherical nucleus. The inner edges of the cell are often irregular, the cells being of different heights, or they project somewhat

FIG. 122.—Cortex of kidney. $\frac{3}{4}$″ × 4. G.A.H.

1. Vein. 2. Artery. 3. Capillary. 4. Convoluted tubule. 5. Collecting tubule. 6. Bowman's capsule. 7. Glomerulus. 8. Descending tubule or limb of Henle. 9. Ascending limb of Henle.

into the lumen of the tubule.[2] Usually the protoplasm stains somewhat darkly, and is granular.

(2) THE STRAIGHT TUBULES (fig. 123). These are called, after their discoverer, Henle's tubules. They have fewer cells to each tubule, five, six, or seven being the utmost. The cells stain darkly, and also, like the convoluted tubules, project somewhat into the lumen of the tubules. The narrow

[1] The size of the lumen depends on the amount of secretion going on.

[2] The section from which Fig. 122 was drawn had an unusually projecting epithelium.

tubules of Henle have still fewer cells, three or four, they are more flattened, and indeed look something like a capillary, but the protoplasm is granular and darkly stained.

(3) THE COLLECTING TUBULES (fig. 123). These are distinguished from the secreting tubules, by having clear protoplasm with cells that are of the same height. Indeed, these tubules look like, and are, ducts. As the tubules get larger, the lumen also becomes larger and larger, and there are more

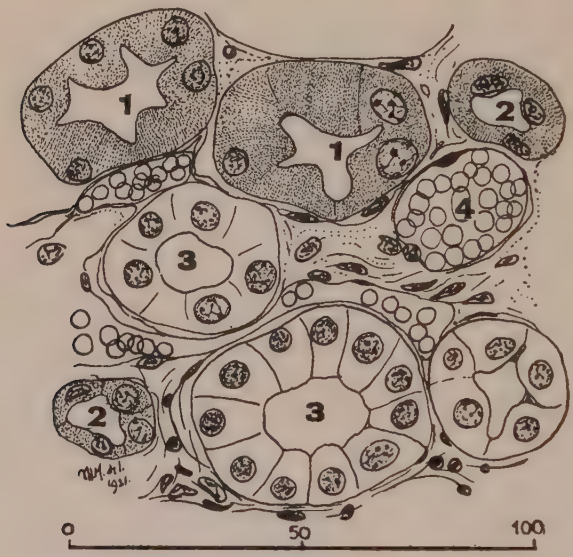



FIG. 123.—Section across part of a medullary ray of kidney. $\frac{1}{8}''$ × 4. G.A.H.

1, 1. Ascending tubules or limbs of Henle. 2, 2. Descending tubules. 3, 3. Collecting tubules. 4. Capillary.

cells in the walls of the tubule. In a tangential section of the kidney, which passes deeply enough to include some Malpighian bodies, we meet here and there in the mass of convoluted tubules pin-cushion-like areas consisting of straight tubules only, these are the medullary rays. The collecting tubules are usually towards the outside of this area with the descending and ascending loops of Henle, together with many blood vessels in the middle.

**The Prostate Gland**—In the male there is a gland surrounding the urethra at its exit from the bladder, of the size and shape of a chestnut. It is covered with a thick fibrous

capsule which includes much unstriped muscle. From the capsule trabeculæ pass downwards into the substance of the gland. There is a large development of unstriped muscle beneath the capsule, and it extends everywhere throughout

FIG. 124.—Prostate gland. $\frac{3}{8}$" × 4. G.A.H.

1. Stroma consisting of connective tissue in which is an enormous amount of unstriped muscle fibre, in the drawing mainly longitudinal. 2. Bundle of unstriped muscle cut transversely. 3, 3. Alveoli. 4. Concretion. 5. Capillary.

the gland around the alveoli, forming its most characteristic feature. Above the urethra, the gland consists of practically muscle only, and under the urethra, close to the bladder, the muscle is present in very large amounts. Farther away the glandular elements increase and the muscle diminishes, but

is always most prominent. Fig. 124 represents an intermediate stage.

The alveoli of the glands are irregular tubes, with very frequent projections into the lumina. These sometimes anastomose to form a network. Consequently the appearance of the prostate gland under the microscope is very variable and irregular.[1] The epithelium lining the alveoli is usually two cells deep; the deeper cells are small and polygonal, the superficial cells are columnar. The general appearance of the epithelium is irregular, there being projections of thickened epithelium at frequent intervals into the large lumen of the alveoli. Within the lumina of the alveoli of the adult gland are frequently found concretions—the so-called amyloid bodies—consisting of a colloid material giving the usual protein tests (see fig. 124).

## THE OVARY AND TESTIS

Two glands producing free cellular elements, and thus unlike the immediately preceding glands, may be considered

FIG. 125.—Hand lens view of a section of an ovary. × 6. G.A.H.

1, 1. Graafian follicles (advanced). 2. Immature Graafian follicle. 3. Highly convoluted blood vessels characteristic of ovary.

here. These are the ovary and testis. It is reasonable to consider the Fallopian tube as the duct of the ovary, although it is not really a part of that gland. And clearly the testis has a duct, and so comes into the present category.

[1] It is not uncommon that the student confuses this gland with the thyroid, the mammary and the lung! The epithelium and the muscular tissue should save him from such an identification.

**The Ovary**—The ovary is a small bean-shaped body between one and one and a half inches long, with a thickness of a quarter to half an inch (fig. 125). It appears white and solid. On the surface of the adult ovary clear vesicles are seen, which project a tiny way above the general contour of

Fig. 126.—Ovary. $\frac{3}{8}'' \times 1$. G.A.H.

1. Immature Graafian follicles. 2. More mature follicle cut obliquely. 3. Blood vessels.

the organ; these are the ripening Graafian follicles. At the same time, yellowish masses are seen in a similar position, which are the yellow bodies or corpora lutea. These take the place of the ruptured Graafian follicles and, when the ovum which the latter liberates is fertilized, hypertrophy and

persist throughout the whole period of pregnancy. Normally they disappear within twelve days, and give rise to small white bodies, the corpora albicantia. The ovary is covered with a layer of columnar to pear-shaped epithelial cells, and these dip down in places into the body of the gland, into the stroma. The stroma consists of closely packed cells like those of embryonic connective tissue. The storma is more dense towards the surface and forms the tunica albuginea. The epithelial cells which dip beneath the surface are ultimately cut off by the stroma cells into little islets, and one of the cells of an islet becomes an ovum. The other cells, arranging themselves round the ovum, give rise to Graafian follicles. These are to

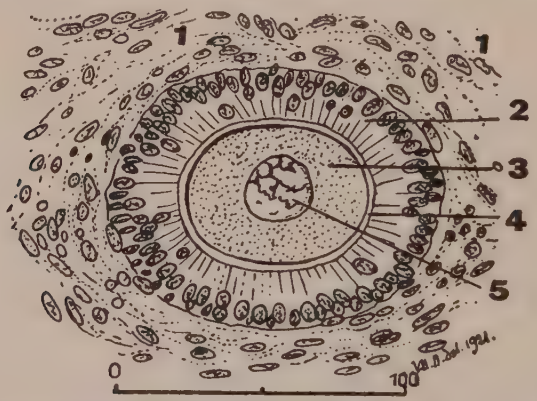



FIG. 127.—Graafian follicle at an early stage. $\frac{1}{6}$" × 2. G.A.H.

1, 1. Connective tissue stroma of ovary. 2. Epithelial cells of Graafian follicle. 3. Ovum with its zona pellucida, 4, and its nucleus, 5.

be seen in all stages of development throughout the ovary (fig. 126). The smaller Graafian follicles are near the surface, the larger ones deeper, though in the end they extend up to the surface and rupture through it and discharge the ova which they contain. Immature Graafian follicles consist of an ovum surrounded by one layer of radially disposed cells (fig. 127). The ovum itself is a large cell, with at first no obvious membrane around it, but soon one appears, and eventually reaches the thickness of about 5$\mu$. It is clear and shining, and so is called the zona pellucida. Because minute pores permeate it in a radial direction, corresponding roughly with the zone of cells around it, it appears radiate in structure, and so is sometimes called the zona radiata. Immediately

within this is a thin membrane. This covers the body of the cell known as the vitellus or yolk. The yolk contains small shining globules of a lipoid nature. The nucleus of the ovum

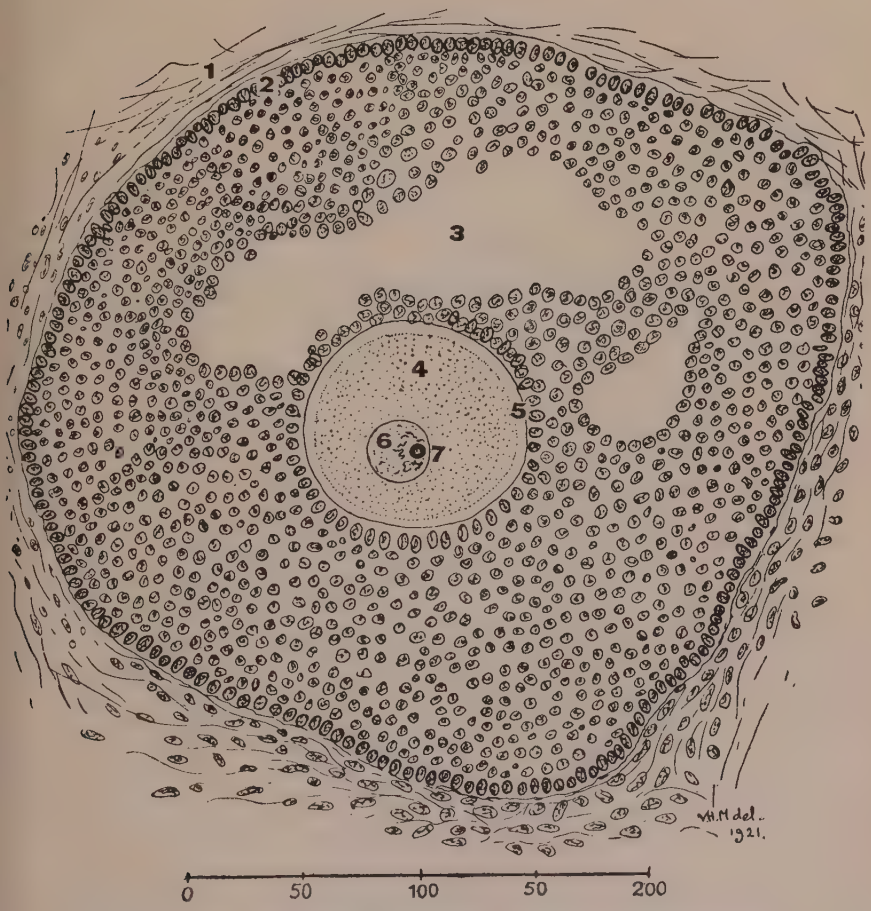



FIG. 128.—Graafian follicle with the liquor folliculi just appearing. $\frac{1}{8}'' \times 2$. G.A.H.

1. Stroma of ovary, forming the theca of the follicle. 2. Membrana granulosa. 3. Liquor folliculi. 4. Ovum. 5. Zona pellucida. 6. Nucleus or germinal vesicle. 7. Nucleolus or germinal spot.

is large, measuring as much as 30$\mu$ across. It contains sharply defined chromatin and a large nucleolus called the germinal spot. The nucleus itself is termed the germinal vesicle. It is unusual

FIG. 129.—Part of a Graafian follicle nearly mature. $\frac{1}{2}$" × 2. G.A.H.
1. Discus proligerus. 2. Ovum. 3. Liquor folliculi. 4. Membrana granulosa. 5. Theca of follicle consisting of a thickened part of the stroma of the ovary.

to see mitotic figures in the ovum, as these take place either earlier in its history or after it has left the Graafian follicle.

First there is only one layer of cells around the ovum. These cells multiply rapidly, forming first of all two layers, one around the ovum and one which lines the follicle. Then, as the follicle enlarges, these multiply enormously, forming a dense mass of cells between the ovum and the wall of the follicle, or theca (fig. 128). As the follicle expands the cells no longer fill the whole of it. The space left is filled by the

FIG. 130.—Part of large corpus luteum. $\frac{2}{3}'' \times 2$. K.C.W.

To the left is seen the ordinary stroma of the ovary with several small Graafian follicles. The rest of the drawing shows one-quarter of the whole corpus luteum.

liquor folliculi. In such a follicle the ovum is surrounded by a mass of cells, the discus proligerus, and a neck of cells (see fig. 129) attach it to the second mass of cells, the membrana granulosa, which completely covers the whole of the inner wall of the follicle. The space between the two sets of cells is filled by liquor folliculi.

With the expansion of the follicle the stroma above it thins, until, when the follicle is ripe, this thin membrane covering it bursts, and the ovum is extruded into the abdominal cavity.

The ruptured epithelial layer comes together and there is considerable extravasation of the blood into the follicle. The subsequent history of the follicle depends on whether the ovum is fertilized and fixates on the wall of the uterus or not. If it does not fixate, a transient corpus luteum is formed. If it does, there is hypertrophy of the walls of the empty follicle, and there is in addition a development of blood vessels and fibrous tissue. The whole of the interior of the follicle is occupied by a jelly-like connective tissue. Strands of

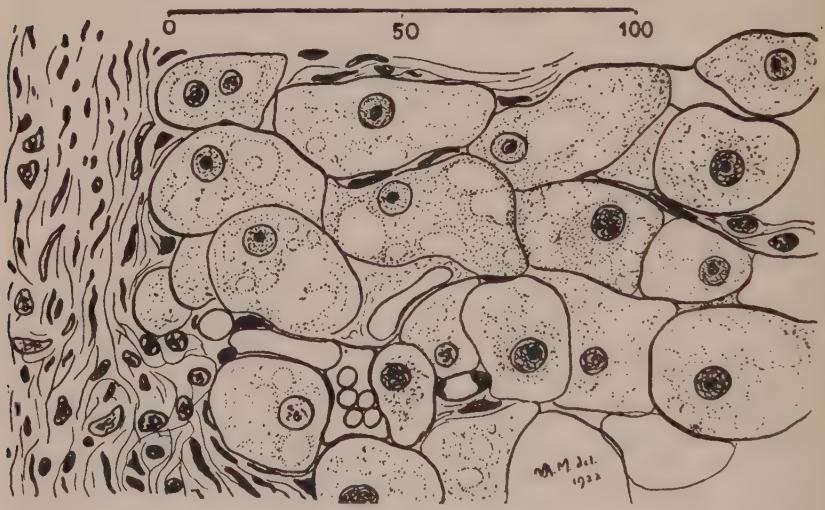



FIG. 131.—High power ($\frac{1}{8}$″ × 4) view of the edge of the corpus luteum of fig. 130.

To the left is the fibrous stroma of the ovary; to the right, luteal cells with connective tissue strands and capillaries running radially. Note the great size of the cells: the largest being approximately 50$\mu$ long.

fibrous tissue and their accompanying blood vessels converge towards the centre of this area, so that finally we have a fibrous framework with a radial disposition, with, in between this, trabeculæ of large yellowish cells and capillary blood vessels (figs. 130 and 131). The arrangement is reminiscent of the cortex of the suprarenal (see fig. 145). The corpus luteum is sharply differentiated from the surrounding ovarian stroma by the theca, but after a time is less sharply marked off, and gradually merges into the stroma and disappears. There is a large vascular supply to the ovary, veins and arteries running

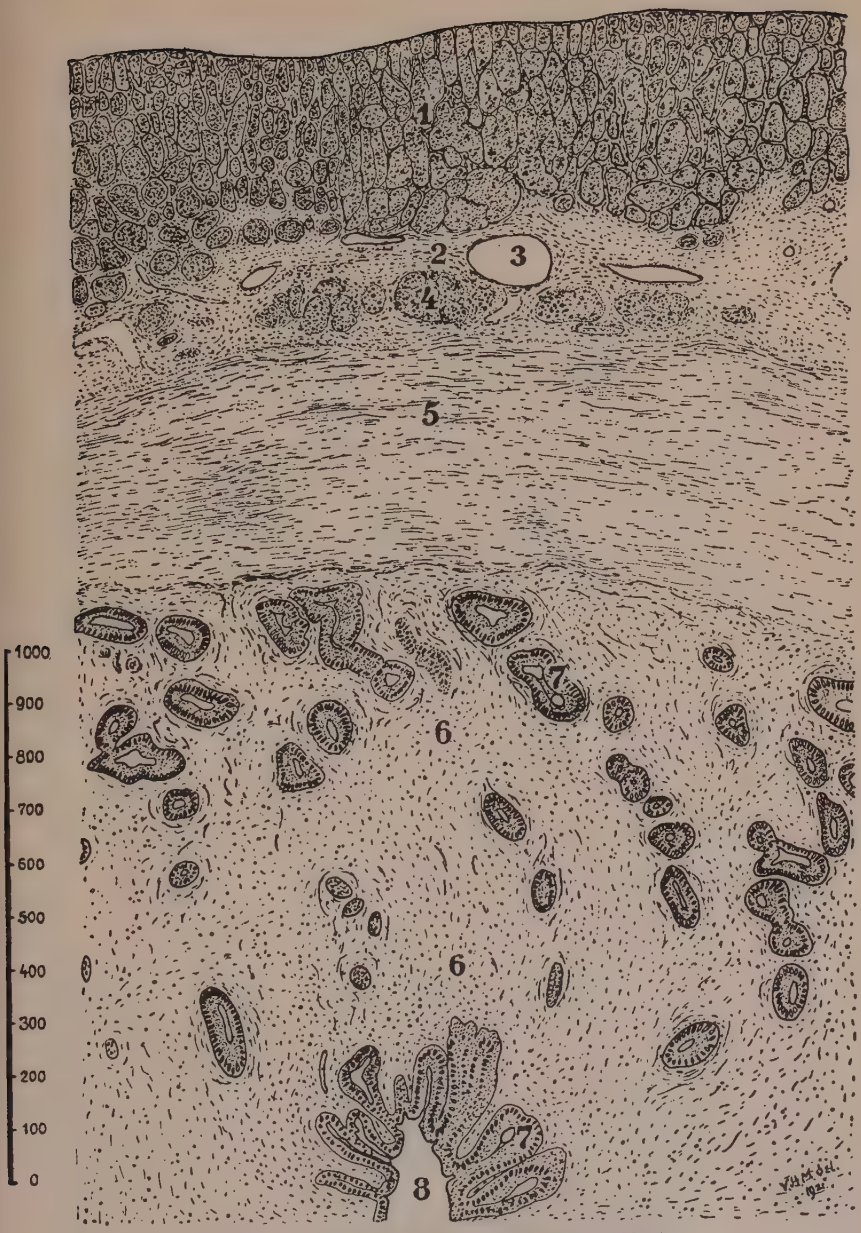



FIG. 132.—Transverse section of uterus (dog).

1. Outer longitudinal muscle coat. 2. Submucous coat containing many blood vessels. 3. Vein.
4. Thin longitudinal muscle coat } Forming the muscularis mucosæ.
5. Thick circular " "
6. Mucous membrane. 7. Glands of mucous membrane cut obliquely, but reaching from its deepest layer to the surface. 8. Lumen of uterus.

in a very tortuous manner (see fig. 125). Investing each Graafian follicle is a close network of capillaries, and in the corpora lutea blood vessels arising from these penetrate in a radial direction.

For a description of the Uterine glands (fig. 132), see later, p. 196.

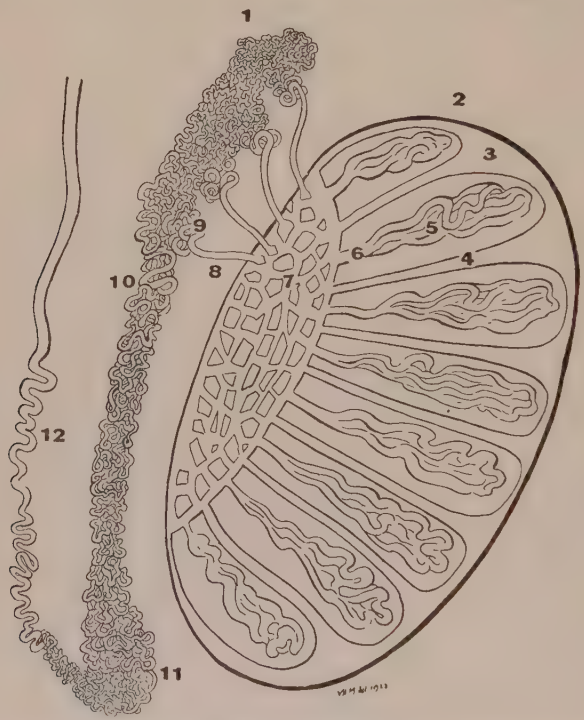



FIG. 133.—Rough diagram to illustrate the structure of testis and epididymis (after Cunningham).

1. Head of epididymis, consisting of a contorted tube into which 15 or 20 convoluted vasa efferentia pour. 2. Testis. 3. Tunica albuginea dipping down between the lobules of the testis. 4. One of the septula from the tunica albuginea. 5. Contorted tubules (tubuli contorti). 6. Straight tubules (tubuli recti). 7. Rete testis. 8. One of the 15–20 vasa efferentia. 9. Coiled part of an efferent vessel forming the conus vasculosus. 10. Epididymis. 11. Tail of epididymis. 12. Ductus deferens.

**The Testis**—The testis is a tubular gland, the tubules of which are larger than those of the kidney, and much longer (fig. 133). Over the testis is a tough membrane of white fibrous tissue containing a large amount of elastic material. This coat is called the tunica albuginea. The tubules (tubuli contorti) are divided into lobules by septa, which extend down

from the tunica albuginea, towards the mediastinum testis. Underneath the tunica albuginea and covering the septa is a loose vascular tissue, which carries the blood vessels down into the body of the testis. The tubuli contorti are arranged radially from the exterior of the testis, inwards towards the mediastinum. Probably they are simple tubules ending

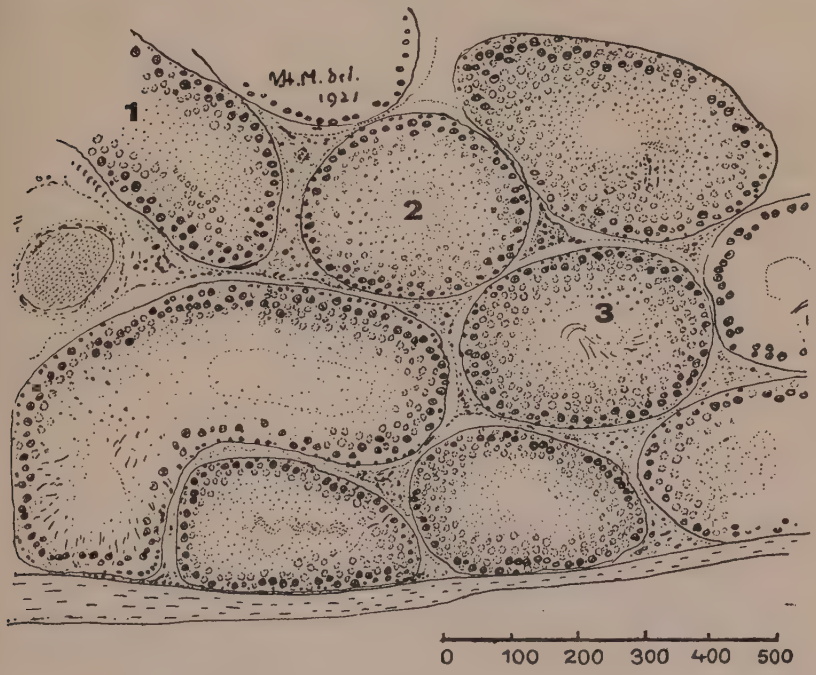



FIG. 134.—Testis. $\frac{2}{3}$" × 2. C.

1. Tubule cut obliquely. 2. Tubule cut transversely. 3. Tubule with a few mature spermatozoa in the lumen. The darkly stained nuclei are evidence of nuclear unrest, preceding or following mitosis.

blindly. They pass into the tubuli recti, and these into a series of passages in the mediastinum testis called the rete testis. These open into the vasa efferentia, which then pass their contents by means of the coni vasculosi (a dozen or more) to the epididymis, a very long tube of increasing diameter, which passes from the upper end of the testis down towards the lower. The epididymis is six to eight metres long, and ultimately passes into the vas deferens, which connects the

epididymis with the seminal vesicles and the ejaculatory duct.

When we turn to the more intimate structure of the testis, we see a number of highly convoluted tubules lying close together, with a small amount of connective tissue in between

FIG. 135.—High power ($\frac{1}{8}$″ × 4) view of the edges of two tubules of the testis with interstitial (intertubular) tissue between.

1. Basement membrane. 2. Spermatocytes. 3, 3. Spermatocytes dividing. 4, 4. Karyokinetic or mitotic figures of dividing spermatocytes. 5, 5. Spermatogonia. 6. Cell of Sertoli. 7. Interstitial cell of Leydig. 8. Four fairly mature spermatozoa attached to a cell of Sertoli.

(fig. 134). In this connective tissue are the usual connective tissue cells, but in addition there are cells that look like epithelial cells, nucleated and containing a small amount of yellow to brownish pigment. These are the interstitial cells of Leydig. They are comparable with the epithelial cells of the endocrine (ductless) glands (see later).

Around each tubule is a basement membrane containing elastic fibres as well as white fibrous tissue. On the basement membrane there is a layer of cubical epithelium. At very regular intervals one of the cells will be seen to contain a darkly staining nucleus (fig. 135). These cells are specialized cells called the spermatogonia. As the dark staining of their nuclei indicates, these cells are in a state of unrest preceding mitosis, and on dividing give rise to a layer of special cells called the spermatocytes. These cells, in their turn, are also in a state of unrest, and their nuclei stain darkly. In this region mitotic figures are easily made out. These spermatocytes on division give rise to rather smaller cells called the spermatids, which go into a resting state. They are then gradually transformed into spermatozoa. The chromatin of the nucleus collects at one pole, and an outgrowth of the tail takes place from a double centrosome in the body of the cell, which forms the neck of the spermatozoon. A considerable amount of the cytoplasm is supposed to be lost in the process. During growth the spermatozoon affixes itself to specialized cells of the cubical epithelium lining the tubule. These cells are the cells of Sertoli. As the spermatozoa become more mature, the cells of Sertoli apparently elongate and raise the spermatozoa into the free lumen of the tubule. The spermatozoa detach themselves and are set free, thence to pass through the straight tubules, the rete testis, and the vasa efferentia into the epididymis and so out to the exterior. The individual spermatozoon in man is 50$\mu$ to 60$\mu$ long (fig. 136). It has an oval, flattened, wedge-shaped head 4$\mu$ to 5$\mu$ long, a neck formed from the cytoplasm of the spermatid and a tail some 45$\mu$ long, extending from

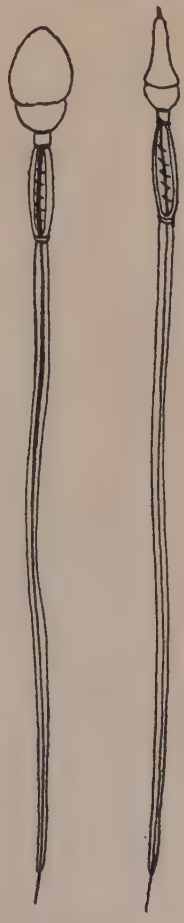


Fig. 136.—Diagram (after Meeves) of two human spermatozoa; the one to the left is seen from the front, the other from the side. Very highly magnified (approximately 2,000$\mu$, or more than three times that of fig. 135).

a centrosome in the cell body or neck of the spermatozoon.

## GLANDS WITH DUCTS OPENING ON TO THE SURFACE OF THE BODY

**The Mammary Gland**—The mammary gland is a gland composed of about twenty small racemose glands, each of

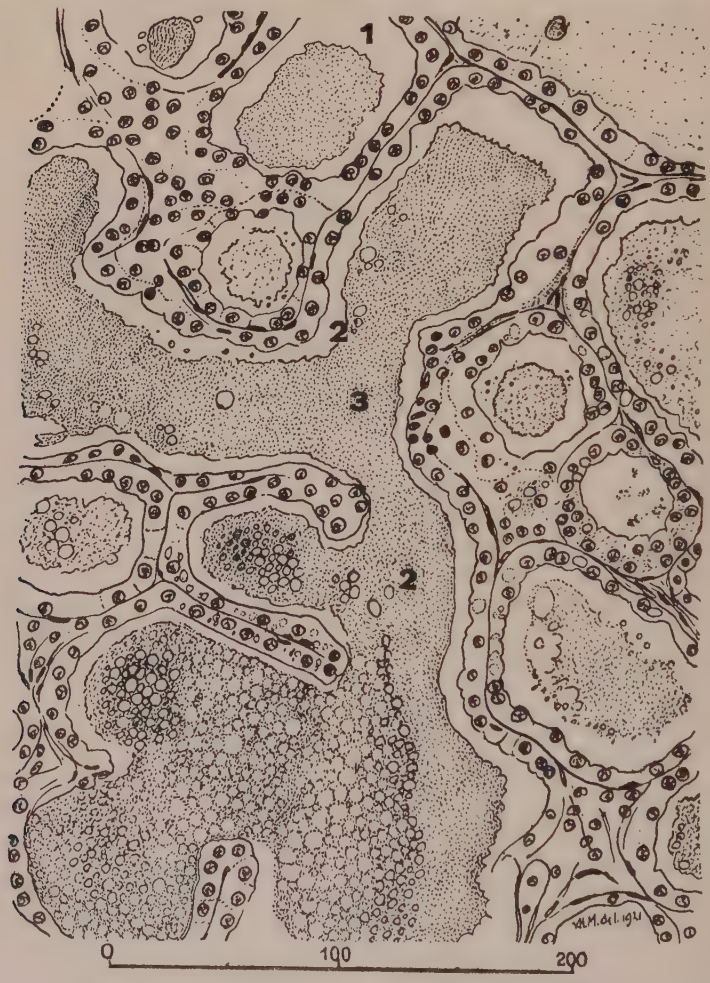



FIG. 137.—Active mammary gland. $\frac{1}{6}'' \times 1$. G.A.H.

1. Alveolus with secretion. 2. Duct with several alveoli opening into it. 3. Coagulated secretion.

which pours its secretion through its own duct (lactiferous duct), which opens at the apex of the nipple. Close to their

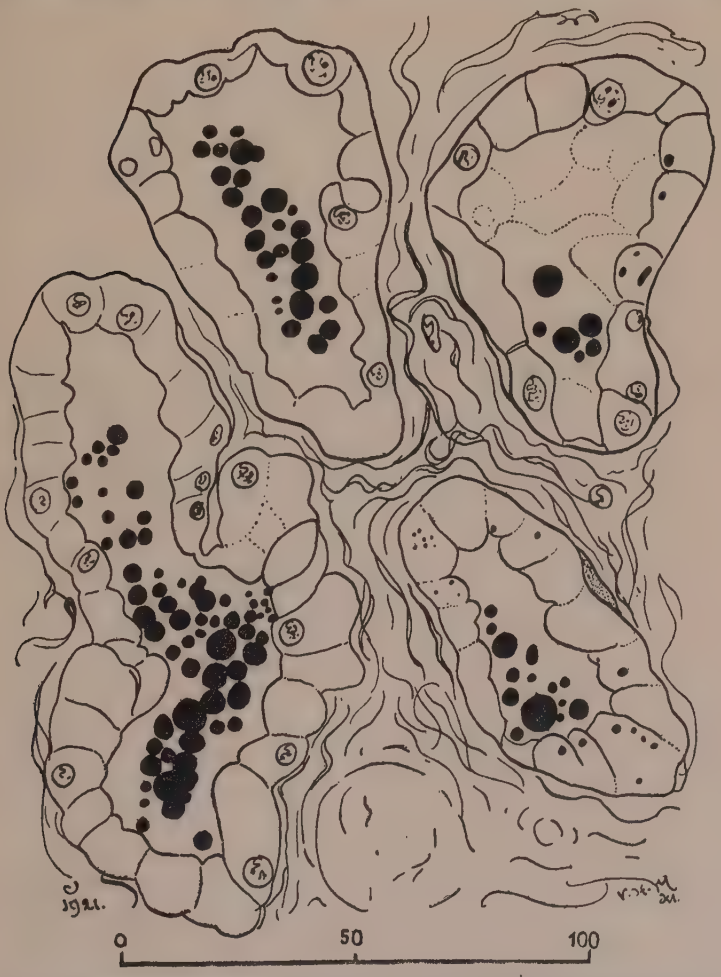



Fig. 138.—Mammary gland (human), active and fixed with osmic acid to show the fat. $\frac{1}{4}'' \times 4$. G.A.H. The latter is visible not only in the middle of the alveoli (i.e. in the secretion) but also in the cells.

mouths these ducts possess a dilatation known as the ampulla or sinus. Separating the small glands is connective tissue, rather coarse and fibrous and containing adipose tissue.

The gland varies very naturally with its state of activity. In the virgin animal the connective tissue predominates and the alveoli of the glands are filled with a mass of polyhedral cells. There is a thick basement membrane around the alveoli, with what looks like unstriped muscle fibres in close proximity to it. In the active gland the picture is quite different. The connective tissue is now in the background. The alveoli are distended and pressed close against each other (fig. 137). They are lined with a cubical to columnar epithe-

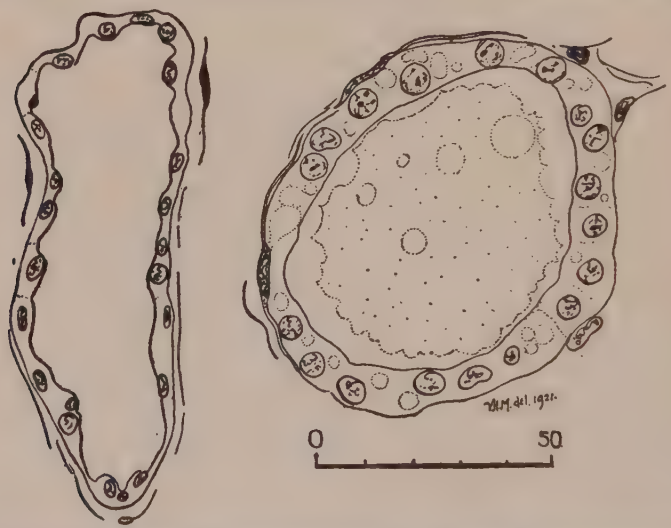



FIG. 139.—Two alveoli of mammary glands. The one to the left is inactive; the one to the right, active. Note the difference in the nuclei, the height of the epithelium, the fat vacuoles in the protoplasm, and the secretion in the lumen of the alveolus.

lium, somewhat ragged at the edges. The cells have large, well-staining nuclei and appear vacuolated. The vacuoles clearly contain fat, as may be proved by fixation of the gland in osmic acid (fig. 138). Within the wide lumen of the alveoli there is milk secretion, usually appearing in the fixed preparation as a mass having the general appearance of ground glass, but with many clear spherical vacuoles from which the fat has been dissolved. The alveolus of a gland that has relapsed into quiescence has flattened subcubical epithelium and nuclei, and the protoplasm and the possible serous fluid in the lumen are not vacuolated.

It will be seen from a comparison of figs. 137 and 139 with figs. 142 and 143 that there is a superficial likeness between an active mammary gland and the thyroid. The main differences are : the mammary gland has alveoli that often branch, whereas those of the thyroid rarely do ; the secretion of the mammary gland is more granular and vacuolated than that of the thyroid ; there is a basement membrane round each alveolus of the mammary gland, which is absent in the thyroid, and the epithelium of the alveoli is more ragged than

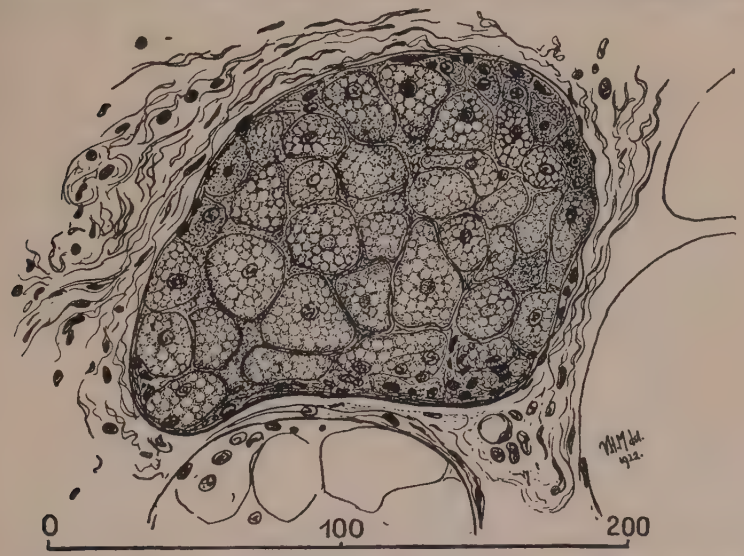



FIG. 140.—Section passing through the body of a saccule of a sebaceous gland. $\frac{1}{8}'' \times 2$. G.A.H.

Note the vacuolated appearance of the cells due to the solution in xylol or chloroform of their waxy secretion in the process of embedding. Parts of three other glandules are indicated. See also Fig. 189.

that of the thyroid. The student will find the two first criteria the best by which to judge.

**Sebaceous Glands**—These are small saccular glands found only (with the exception of the labia minora and the eyelids) where there are hairs on the skin, into the follicles of which they open. The glands have short ducts into which open two, three, four, up to twenty recesses, the secretory saccules. Each saccule is filled with epithelial cells, which contain a large amount of fat-like globules. (Really the globules consist of wax (fig. 140).) The deeper cells are continually multi-

plying, and push the older cells towards the centre of the saccule. Here they disintegrate, and their disintegration products form the secretion of the glands. This is pushed by the growth of the cells behind out into the duct of the gland,

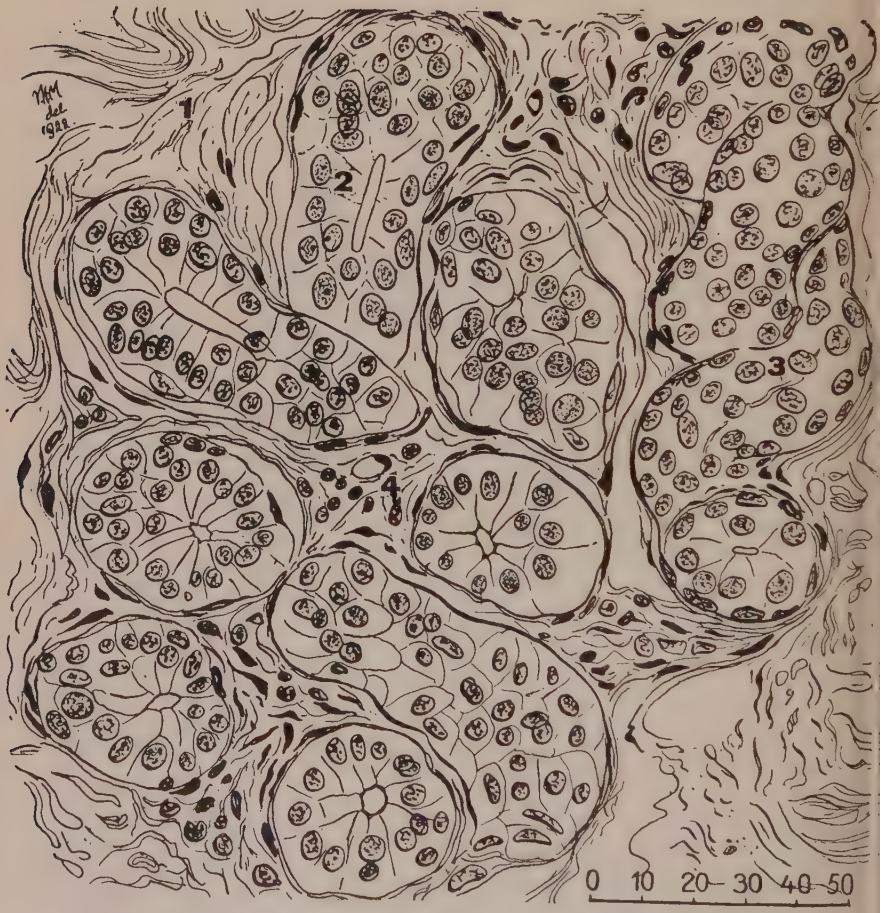



FIG. 141.—Sweat gland. $\frac{1}{8}''$ × 4. K.C.W. (See also Fig. 187.)

1. Dense connective tissue of the true skin. 2. Alveolus of sweat gland cut obliquely. 3. Alveolus showing typical twisted appearance. 4. Capillary.

thence into the mouth of the hair follicle, and so on to the skin (cp. fig. 189).

Large sebaceous glands are found in the meatus of the

external ear in close relation to the ceruminous or wax glands. The latter from their appearance and development are to be regarded as modified sweat glands.

**Sweat (or Sudoriferous) Glands**—The sweat glands consist of two parts : the gland proper, which lies in the true skin and the duct of the gland (see fig. 187). The gland proper consists of a tube, blind at the lower end and coiled into a ball (fig. 141). This tube is lined with a single layer of cubical or columnar epithelium with, at times, pigment granules in it. Immediately external to this is a layer of what looks like unstriped muscle wrapped circularly round the gland. Outside of this is the basement of membrane. There is a large blood supply to the gland, and nerve fibres have been traced into the secretory cells. In the larger glands (of the axilla, etc.) the tube of the gland often bifurcates repeatedly.

The duct in the true skin is often narrower than the gland itself, and is lined by two or more layers of small epithelial cells. The twisted corkscrew part of the duct in the stratified epithelium of the skin is merely a channel passing between the epidermal cells.

## GLANDS WITH NO OBVIOUS DUCTS

Throughout the body there are to be found glands with no conceivable vestige of a duct, and these have naturally been termed ductless glands. It was found that a number of them apparently secreted something into the blood stream, and so they have been called the glands of internal secretion, or the endocrine organs (which means the same thing). Because their function of secretion is hidden they are sometimes called the cryptorhetic glands. Conversely, some glands that have an internal secretion have been called ductless glands, even though they possess obvious ducts (i.e. the pancreas). In fact, to-day, when we speak of the ductless glands we do not mean glands which have no ducts, but glands which have an internal secretion.[1]

We have above divided the glands with no obvious ducts into two classes : those in which the fixed epithelial elements are predominant, and those in which the free cellular elements

[1] This again illustrates the illogicality of our terminology and the confusion between morphological and physiological terms.

are predominant. This classification is roughly parallel to a division into endocrine organs on the one hand, and lymphoid and adenoid tissue on the other.

## DUCTLESS GLANDS WITH FIXED CELLS PREDOMINANT

Of these the most important are the thyroid (with the parathyroid), the suprarenal, and the pituitary glands. Less

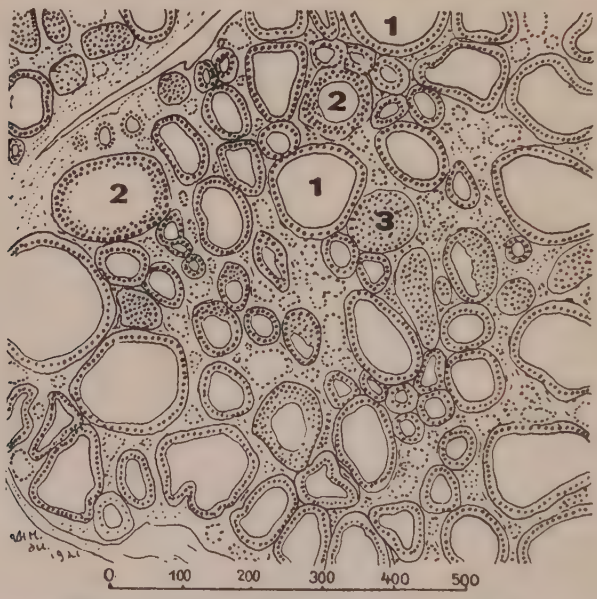



FIG. 142.—Thyroid gland. $\frac{2}{3}$″ × 2. G.A.H.

1, 1. Spherical alveoli cut at the equator. 2, 2. Alveoli cut nearer the pole. 3. Tangential section of an alveolus.

important are the pineal body, the carotid gland, and the accessory suprarenals.

The thyroid is a gland situated in the neck, external to the larynx. It consists of two lobes with an isthmus joining them. It is covered by a connective tissue capsule which, dipping down into the body of the gland, divides it into incomplete, irregular lobules. The gland has an enormous blood supply, which comes, as will be seen, into close relation with the cells. (This close relation of the blood supply to the cells is characteristic of all the endocrine organs.) There is, moreover, a

big lymphatic supply as well. Under the microscope the gland is seen to consist of closed spherical vesicles or alveoli of all sizes, see figs. 142 and 143. The vesicles are usually spherical or oval, and very rarely branched (cp. with the

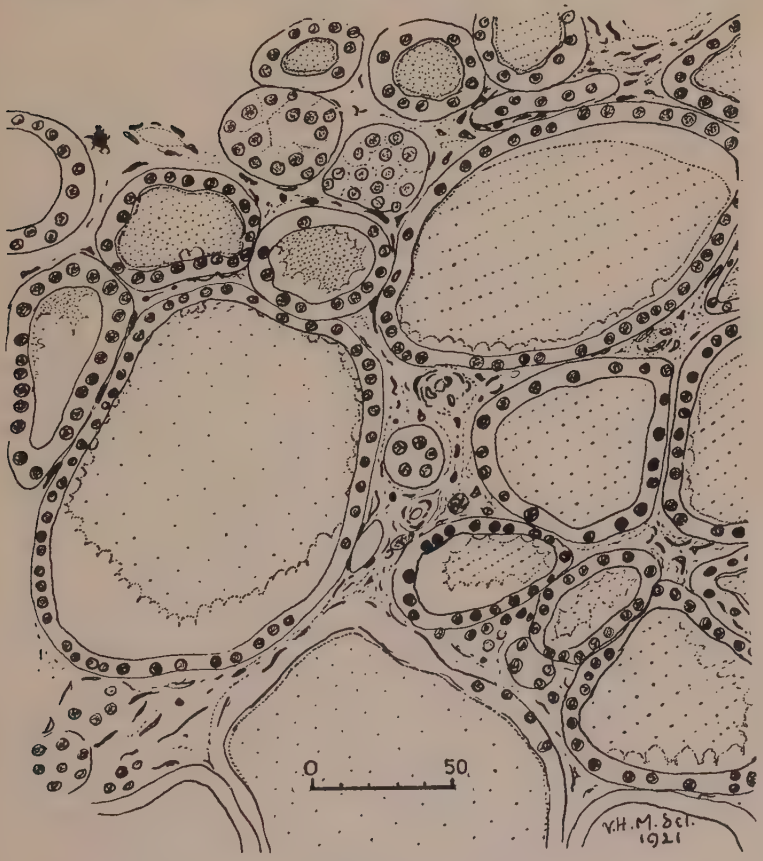



Fig. 143.—Thyroid. $\frac{1}{6}$" × 2. E.C.M.

mammary gland). They are lined with cubical epithelium, with a spherical, well-staining nucleus. Inside the vesicle is a secretion of shining hyaline matter, usually spoken of as a colloid material. Chemically it contains iodine in the form of thyroxin, which is a tri-iodo-indol-proprionic acid. The vesicles have apparently no basement

membrane, and so are placed immediately upon the reticular connective tissue of the gland, in which manifold blood capillaries and lymphatic vessels run. This brings the cells into very close relation, both with the blood and the lymph. Colloid material in the lymphatic channels has been described

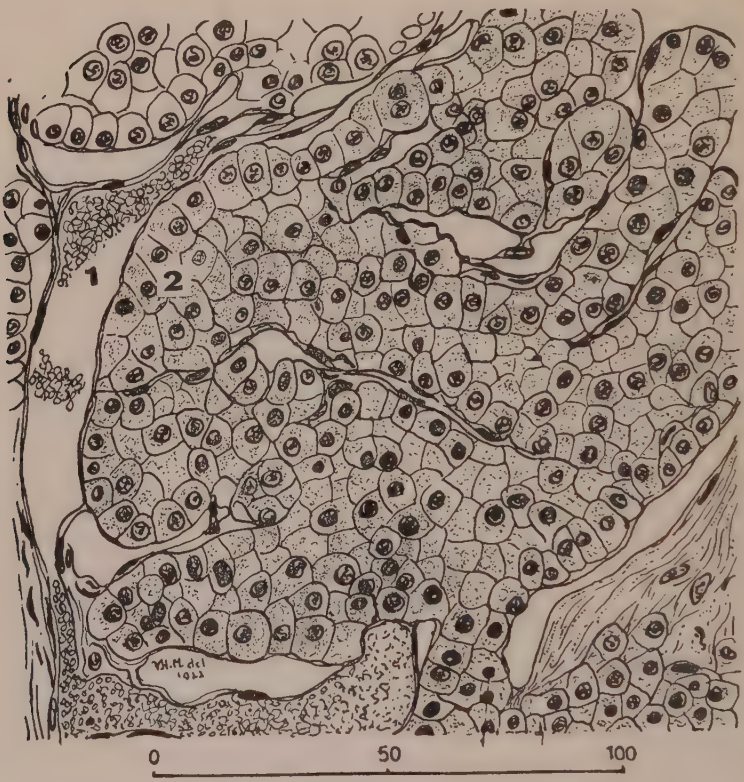



FIG. 144.—Parathyroid. $\frac{1}{6}$″ × 4. W.M.C.

1. Blood vessel with debris of red blood corpuscles. 2. Parathyroid cells arranged in rough trabeculæ with capillaries between.

and it is thought that this is the usual path of secretion. The appearance of the thyroid gland is very dependent upon the food supply to the body. It is as described above when the food material contains iodine. In the absence of iodine the gland enlarges, and the size of the vesicles decreases. In these variations in its microscopic appearance it resembles

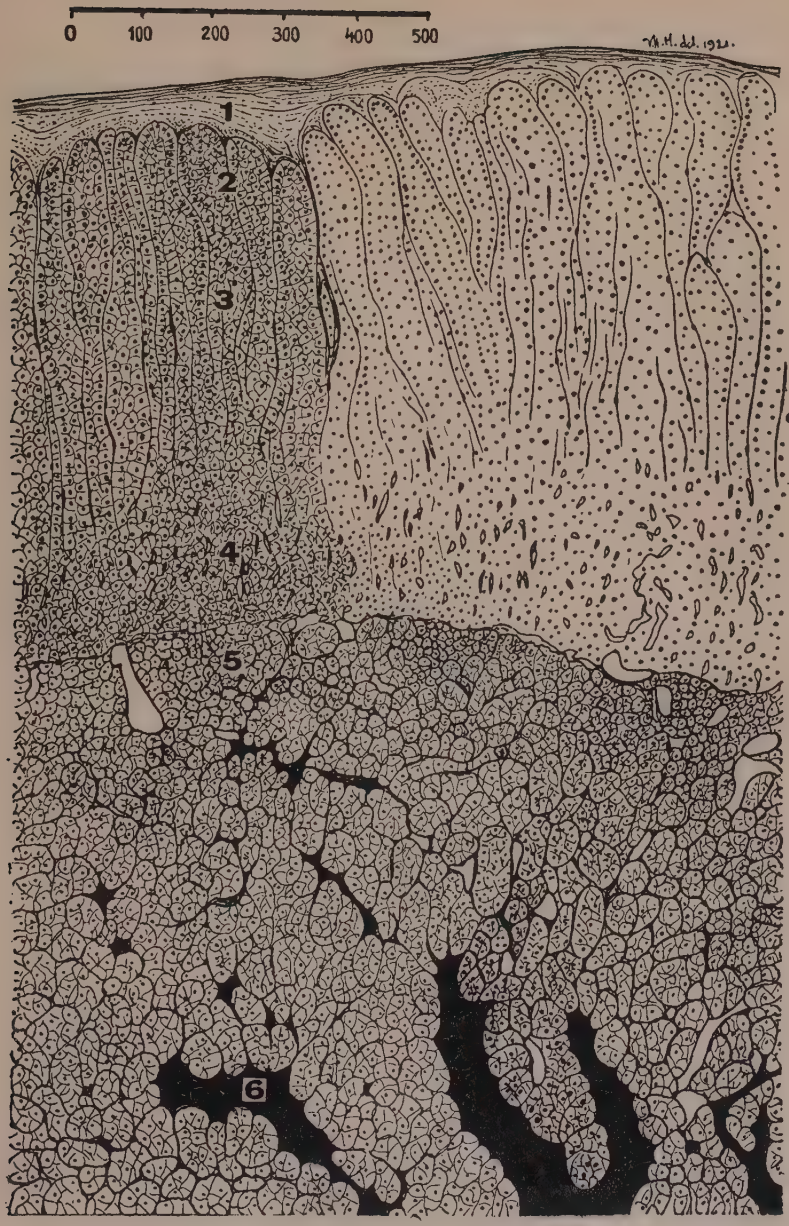



FIG. 145.—Suprarenal showing cortex and medulla. $\frac{2}{3}'' \times 2$. G.A.H.

1. Connective tissue capsule, extending down in between the cortical cells and dividing them into trabeculæ. 2. Zona glomerulosa. 3. Zona fasciculata. 4. Zona reticulata. 5. Medulla. 6, Venous sinuses in between the trabeculæ of the medulla.

the mammary gland, and the student should beware of confusing the two.

**The Parathyroids**—Often in a section of the thyroid, irregular masses of what appears at first sight to be lymphoid material are seen. Closer inspection shows them to consist of "epithelial" or glandular cells. These masses are the parathyroids (fig. 144). Sometimes in man they are embedded deeply in the substance of the thyroid, but usually they are separable from it. Under the microscope they consist of a

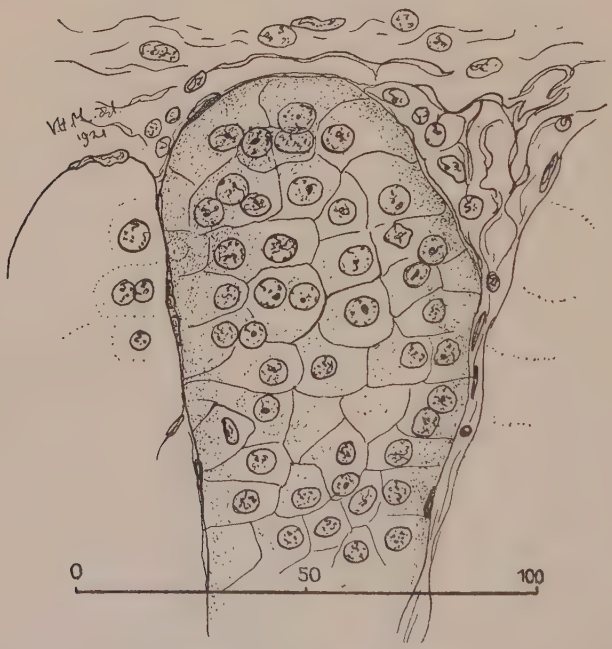



FIG. 146.—Zona glomerulosa of suprarenal cortex. $\frac{1}{6}$" × 4. G.A.H.

highly vascular connective tissue, containing trabeculæ of epithelial or glandular cells. In between the trabeculæ are capillaries closely resembling those in the liver and, as will be seen, those in the suprarenal and pituitary bodies. The capillaries are large, irregular and sinusoidal. There is nothing between the cells and the blood but the thin wall of the capillaries. There can be, on this account, a very rapid passage of material from the blood into the parathyroid cells

or in the opposite direction, a thing which characterizes the ductless glands and the liver.

**The Suprarenal Gland**—Closely applied to the upper pole of the kidney is a gland of a tricornuate shape, receiving a very large blood and lymphatic supply. This, from its position, is called the suprarenal body. In animals other than man, it may be *near* the kidney only, and so is called the adrenal gland. To the naked eye, on section, it consists of two parts, the cortex and medulla. The latter is very much darker in colour, owing to the large amount of blood in its interstices. When we examine the cortex under the microscope we discover that the connective tissue capsule over the gland dips down into the cortex and divides it up in a characteristic way. Externally (see fig. 145), we have rounded masses of tissue called the zona glomerulosa ; further down, the connective tissue extends in parallel lines, the zona fasciculata ; then the columns break up and anastomose the one with the other, forming the zona reticulata. The glandular elements of the cortex are epithelial-like cells, polyhedral in shape, with spherical, well-staining nuclei. The cells often have more than one nucleus. In arrangement they follow the connective tissue. In the zona glomerulosa masses of cells are often arranged radially round what appears like a lumen (fig. 146), but more ordinarily the cells are polyhedral and arranged irregularly. In the zona fasciculata each group of cells of the glomerulosa is represented by two parallel rows of cells (fig. 147). In this neighbourhood the cells are larger,

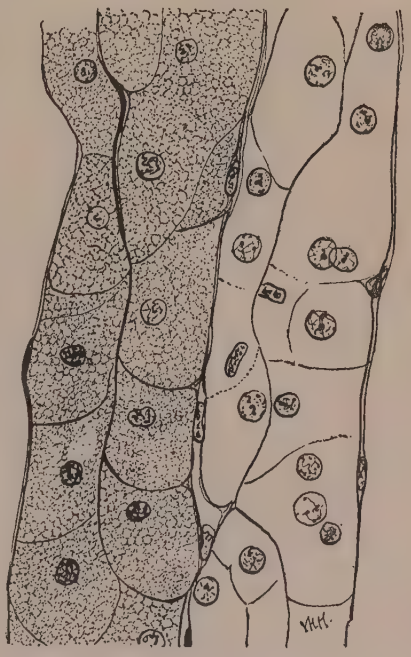


FIG. 147.—Zona fasciculata-suprarenal cortex. $\frac{1}{6}'' \times 4$. G.A.H.

and the protoplasm appears granular. This is due to the fact that in this layer and the innermost layer of the cortex there is a large development of some lipoid material like cholesterol. In the ordinary preparation this would be washed out by xylol, and the protoplasm will appear as if we have

FIG. 148.—Zona reticulata-suprarenal cortex. $\frac{1}{8}$" × 4. G.A.H.

1, 1. Capillaries. 2. Endothelial nucleus of capillary wall. 3. Trabeculæ of rather smaller cells than elsewhere in the suprarenal. 4. Part of medulla.

unstained granules present. In the zona reticulata (fig. 148) there is anastomosis of the trabeculæ, and the cells are here smaller than in the rest of the suprarenal. The irregular anastomosing columns of cells, with their big sinus-like capillaries in between (compare parathyroids, pituitary, islets of

Langerhans), give the suprarenal at this point a marked resemblance to the liver. The blood supply of the suprarenal follows the distribution of the connective tissue in the cortex, for the arteries run down in the connective tissue, break up into capillaries which finally open into the sinusoidal capillaries of the zona fasciculata. These empty into the big sinus

FIG. 149.—Medulla of suprarenal. $\frac{1}{8}$" × 4. G.A.H.

1. Sinus-like capillaries, the endothelium of which is visible in most parts of the preparation. 2. Trabeculæ of large cells, larger than elsewhere in the suprarenal.

Figs. 146–149 are all drawn to the same scale, and from the same suprarenal. Place one above the other, and the range of size and spacing of cells from the connective tissue capsule to the medulla is obtained.

spaces of the medulla. A few arterioles, however, pass right down to the medulla, form capillaries there, and empty into the sinuses. The medulla, then, receives blood from two sources: (1) that which has already passed through the cortex and received or given up material there; and (2) that which is fully oxygenated, from the arteries. (Cp. with the liver.)

The medulla of the suprarenal is a much more sponge-like structure. Its characteristic is the large sinuses (see figs. 145 and 148) that are found in it. These penetrate in between the groups of cells, so that the latter appear almost like ice-floes floating in a sea of blood. The cells are larger than we have met with elsewhere in the suprarenal and form coarse trabeculæ running throughout the medulla (fig. 149). The trabeculæ are more separated, naturally, towards the centre of the medulla. The cells have spherical, well-stained nuclei, the cytoplasm is granular, and, if fixed in chromic acid, takes on a characteristic brown colour. (This characteristic is shared by the cells in the para-ganglia of the sympathetic.) Nerve fibres are sometimes to be seen in the medulla, and also nerve cells of the sympathetic type.

**The Pituitary Gland**—In the pituitary fossa, or sella

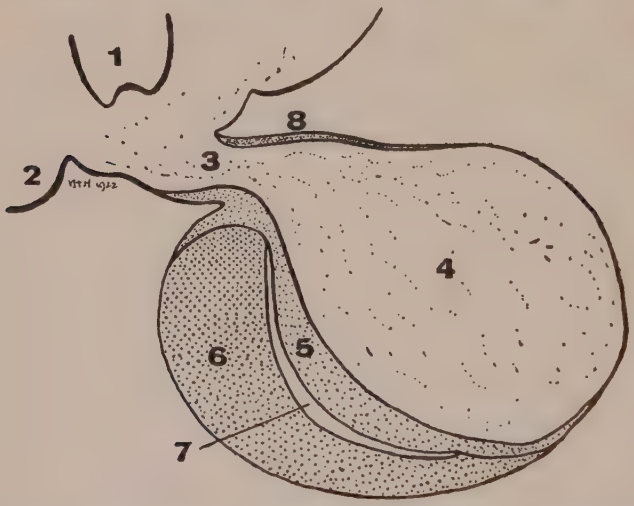



FIG. 150.—Hand-lens view of a section of the pituitary. (After Herring.)

1. Third ventricle. 2. Optic chiasma. 3. Neck of nervous material to 4. Pars posterior or nervosa. 5. Pars intermedia. 6. Pars anterior. 7. Intraglandular cleft. 8. Epithelial cells extending from pars intermedia around the neck of the pituitary body.

turcica, of the sphenoid bone there is a gland the size of a small nut, known as the pituitary body. It consists of two parts: the one derived in the fœtus from the roof of the mouth, and epithelial in nature; the other derived from the brain, and consisting of nervous tissue. The connection of the former with the roof of the mouth is completely cut off,

whereas the latter, nervous, portion is still in connection with the brain. Another name, therefore, for the organ is the hypophysis cerebri. It is connected to the brain by the infundibulum, and is in close relation to the optic chiasma and the third ventricle. The part derived from the roof of the mouth grasps the nervous part much as a hand grasps a ball (fig. 150). The two parts are known from their positions as the pars anterior and the pars posterior. A third portion has been distinguished, the pars intermedia, which lies between the pars anterior and the pars posterior. The distinction

FIG. 151.—Pituitary body. Pars anterior showing epithelial cells arranged in rough trabeculæ (cp. Fig. 144, Parathyroid). $\frac{1}{8}$″ × 4. W.M.C.
1. Capillaries. 2. Eosinophil cells, with dense granulation staining with acid dyes.

is not very important. Some of the cells of the pars intermedia stray up around the neck of the infundibulum. There is, moreover, a cleft between the pars anterior and the pars intermedia, which is not complete and may have no functional significance whatever. Both the pars anterior and the pars intermedia are epithelial in origin, and contain epithelium-like cells. The pars posterior is entirely nervous.

*The Pars Anterior*—This consists under the microscope (fig. 151) of trabeculæ, columns, and irregular masses of cells, mainly ovoid or pear-shaped, comparable to those in the medulla of the suprarenal. Two types, or even three types

of cell may be distinguished. One type stains strongly with eosin, and so may be called eosinophil or oxyphil; another, and more numerous class, stains either coarsely or finely basophil. Between these groups of cells are large sinusoidal capillaries, and the whole of the pars anterior and pars intermedia have a good blood supply.

In the *Pars Intermedia* (fig. 152) the blood vessels are fewer

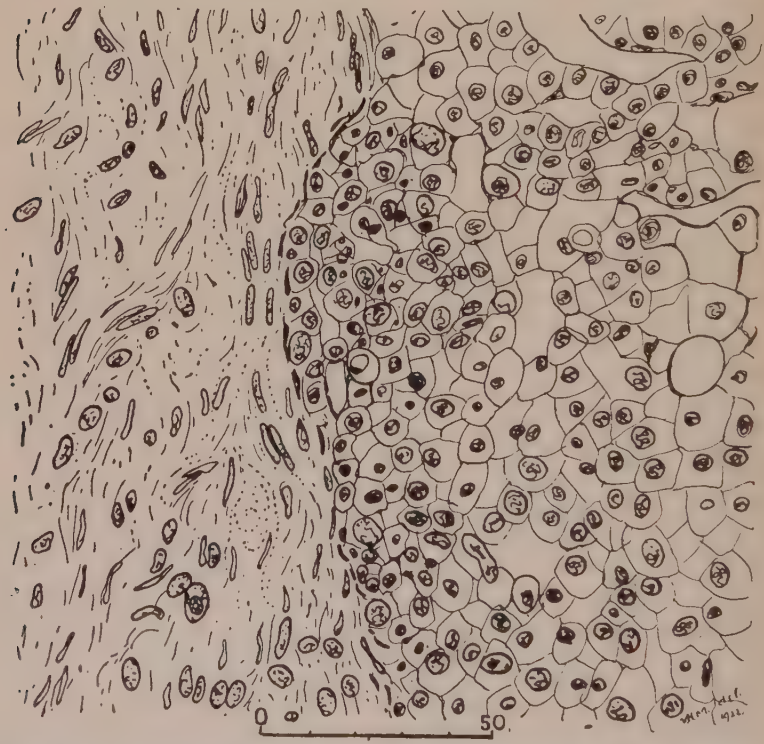



FIG. 152.—Pituitary. Edge of pars intermedia abutting on pars nervosa. To the right are seen the cells of the pars intermedia and to the left the pars nervosa (or pars posterior). $\frac{1}{8}''$ × 4. W.M.C.

and the cells are less granular, or have finer granules. In between the cells there is to be seen hyaline material, and in places where there is a large secretion of this material the cells are grouped round it in a way reminiscent of the thyroid (fig. 153). Indeed, the material is sometimes called the colloid material, like that in the thyroid. The colloid

apparently passes in between the cells and is handed on into the pars posterior.

The *Pars Posterior* (fig. 152) consists almost entirely of the connective tissue characteristic of the central nervous system, the neuroglia. Blood vessels are infrequent, and there are a few nerve fibres scattered about. In between the neuroglial cells and their processes are to be seen masses of

FIG. 153.—Pituitary body. Pars intermedia. $\frac{1}{6}$" × 4. W.M.C.

The cells of the pars intermedia often appear arranged round a mass of colloid secretion, much as are the secretory cells of the thyroid gland (cp. Fig. 143).

colloid material, probably derived from the pars anterior and pars intermedia. It is assumed that this is passing up the infundibulum and into the third ventricle. The relation of this gland to diseases of growth such as acromegaly and gigantism is too well known to need any discussion here.

## GLANDS IN WHICH THERE ARE NO OBVIOUS DUCTS, BUT IN WHICH THE FREE CELLS ARE THE MOST IMPORTANT FEATURE

These glands include the lymph glands, the scattered lymph follicles in the small and large intestine, in Peyer's patches in the lower end of the small intestine, in the appendix, and in the pharyngeal and respiratory regions ; the thymus, and the hæmolymph glands, the most important of which is the spleen.

**Lymph Glands**—These are glands on the course of the lymphatic vessels, examples of which can be found in the elbow, the axilla, the knee, the groin, the neck, the thorax and the

abdomen. Externally they are covered with a thin connective tissue sheath, consisting mainly of white and elastic fibres, but there are usually present some unstriped muscle cells (fig. 154). These last are not an obvious feature. The

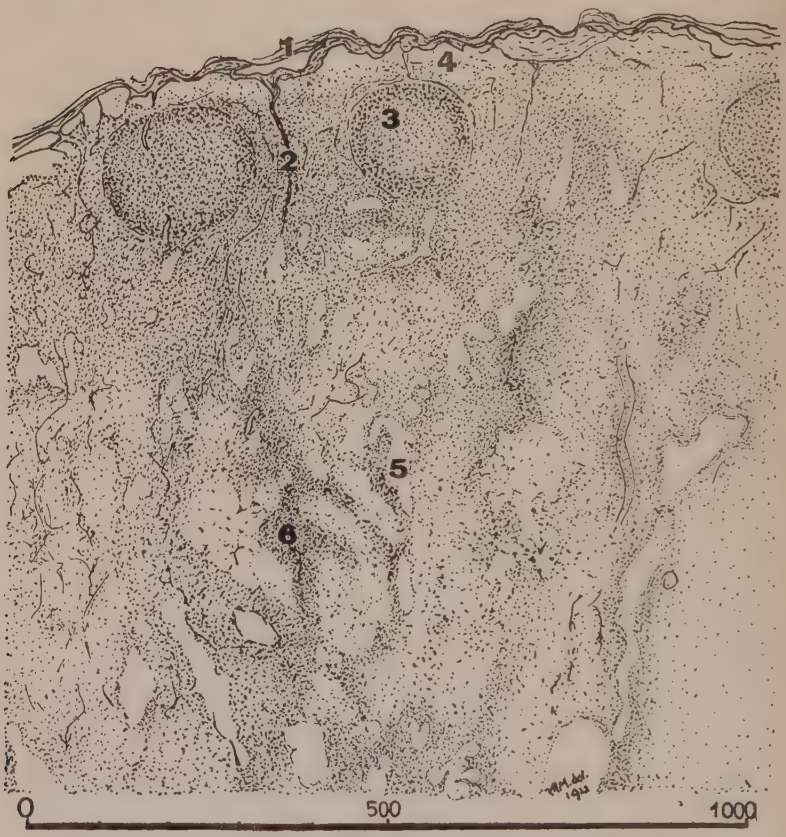



Fig. 154.—Lymph gland. $\frac{3}{8}$″ × 2. K.C.W.

1. Capsule of connective tissue. 2. Trabecula of connective tissue extending down into the body of the gland. 3. Lymph follicle. 4. Lymph path or sinus in cortex. 5. Lymph path in medulla. 6. Lymph "cord" in medulla.

capsule sends in trabeculæ into the cortex, and these trabeculæ branch and anastomose freely, and support the medulla of the gland. The pulp of both cortex and medulla consists of fine reticular material (fig. 32), with masses of lymphocytes in the meshes. There are nodules (lymph follicles) of darkly

staining lymphocytes in the cortex, the outer layers staining more deeply than the interior. Mitotic figures are found in this neighbourhood, and it is thought that here the young lymphocytes are produced. These nodules are termed germinal centres. The dark staining is evidence of karyokinetic activity (fig. 154). Around the trabeculæ the lymphocytes

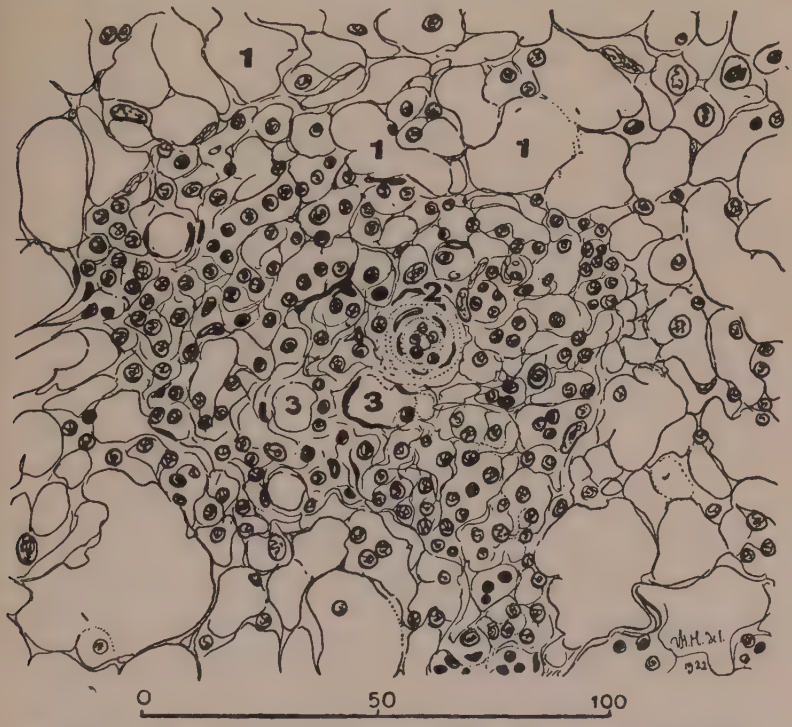



FIG. 155.—Lymph cord and surrounding lymph path from a lymphatic gland. $\frac{1}{8}''$ × 4. K.C.W.

1, 1, 1. Lymph path or sinus. 2. Artery. 3, 3. Capillaries. Compare this drawing with fig. 163, showing the edge of a lymphoid mass (Malpighian body) in the spleen, and note the penetration of red blood corpuscles in the latter into the sinuses of the organ.

are not so numerous, and it is likely that the lymph, which enters the gland through afferent vessels, passes into these spaces called lymph paths, and leaves the gland through the efferent vessels, sweeping along with it the more mature lymphocytes which have migrated from the follicles into the lymph path (fig. 155). Lymphoid tissue receives a large supply

of blood vessels, but these never open out into the sinuses of the organ (contrast the spleen and cp. fig. 155 with fig. 163). The lymph corpuscles have the character of the smaller lymphocytes of the blood, though here and there some of the larger lymphocytes may be seen. Their function is pre-eminently that of taking up foreign bodies which enter the gland, via the lymph, such as micro-organisms and inspired soot. This explains the swelling of lymph glands when lymphatic channels are invaded by micro-organisms.

Scattered lymphatic follicles, comparable to those of the lymphatic glands, are to be found in various of the mucosæ. Single follicles are to be found in the solitary glands of the

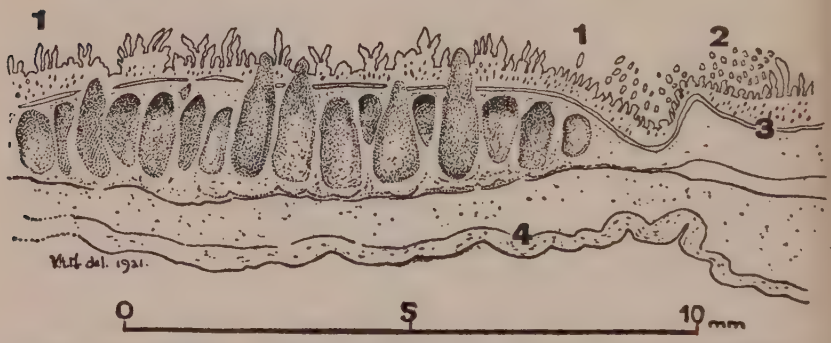



FIG. 156.—Hand-lens view of a section of small intestine showing a Peyer's patch. G.A.H.

1, 1. Peyer's patch (lymphoid material). 2. Ordinary mucous membrane of small intestine. 3. Muscularis mucosæ. 4. Circular and longitudinal muscle of the small intestine.

small and large intestine. These are tiny bodies about the size of a pin's head, which have their base in the submucous coat of the intestine, but push up through the muscularis mucosæ and actually project into the lumen of the gut. Over them, in the small intestine, the villi become either very irregular or disappear. The follicles thrust on one side the crypts of Lieberkühn. They consist of dense reticular connective tissue in the meshes of which are found crowded masses of lymphocytes. Probably the lymphocytes migrate into the lumen of the gut and destroy the micro-organisms found there, or protect the gut wall from invasion.

Sometimes a number of these glands are found side by side in a long strip of the lower end of the small intestine (fig. 156). These patches of lymphoid material are called *Peyer's patches*,

FIG. 157.—Low-power view of a Peyer's patch. $\frac{2}{3}'' \times 1$. G.A.H.

1. Villus cut obliquely. 2, 2. Villi cut longitudinally. 3. Crypts of Lieberkühn. 4. Muscularis mucosæ, sending down strands between the lymphoid material. 5. One of the lymph nodules piercing the muscularis mucosæ and passing up through the mucous membrane to the lumen of the gut. 6, 6. Lymph nodules.

after their discoverer. Their structure is identical with that of the solitary lymph follicles, and no doubt their function is the same. In their outer borders the lymphocytes stain more darkly and mitotic figures are to be found—rapid production of lymphocytes is undoubtedly taking place there (fig. 157). As in the case of the solitary follicles, the villi are much distorted in shape, or may even be absent, over these patches, particularly where they project through the muscularis mucosæ up to the surface of the gut (see fig. 156). Near the neighbourhood of Peyer's patches, the mucous coat contains more lymphocytes than is normal.

In the *appendix* (found in man, in the higher apes, rodents, and the wombat only) we have a hollow organ showing a structure similar to that of the large intestine, in which the whole of the submucous coat consists of masses of lymph follicles. The most probable view of its function is that it is the same as that of the lymph gland, i.e. scavenging.

Other masses of lymphoid tissue are to be found in the upper respiratory tracts, guarding the mouth of the Eustachian tube and in the posterior nares. The latter are sometimes called the pharyngeal tonsils. The lymph tissue is found immediately under the epithelium, which, in the case of the adenoids near the Eustachian tube, is ciliated, but in the pharyngeal portion is stratified. The true tonsils are follicles or nodules of lymphoid tissue closely packed around invaginations of the mucous membrane (called crypts, fig. 158). They are covered with stratified epithelium, which extends down into the crypts at the end of which mucous glands are often found. Mingled with the secretion of these glands are lymphocytes, which have migrated from the lymph follicles, and desquamated epithelium. The follicles are active germ centres, i.e. places where active mitotic division of the lymphocytes is occurring, and there is a rich supply of blood vessels and lymphatics. The function of these glands must be protective, like that of the other lymph glands we have considered. There are other masses of lymphoid tissue in the palate and tongue, which are sometimes spoken of as tonsils.

**The Thymus**—This organ is usually classified with the endocrine organs, chiefly because its functions are mysterious. In its appearance it closely resembles a lymph gland, and is for that reason included with them here. When unravelled it

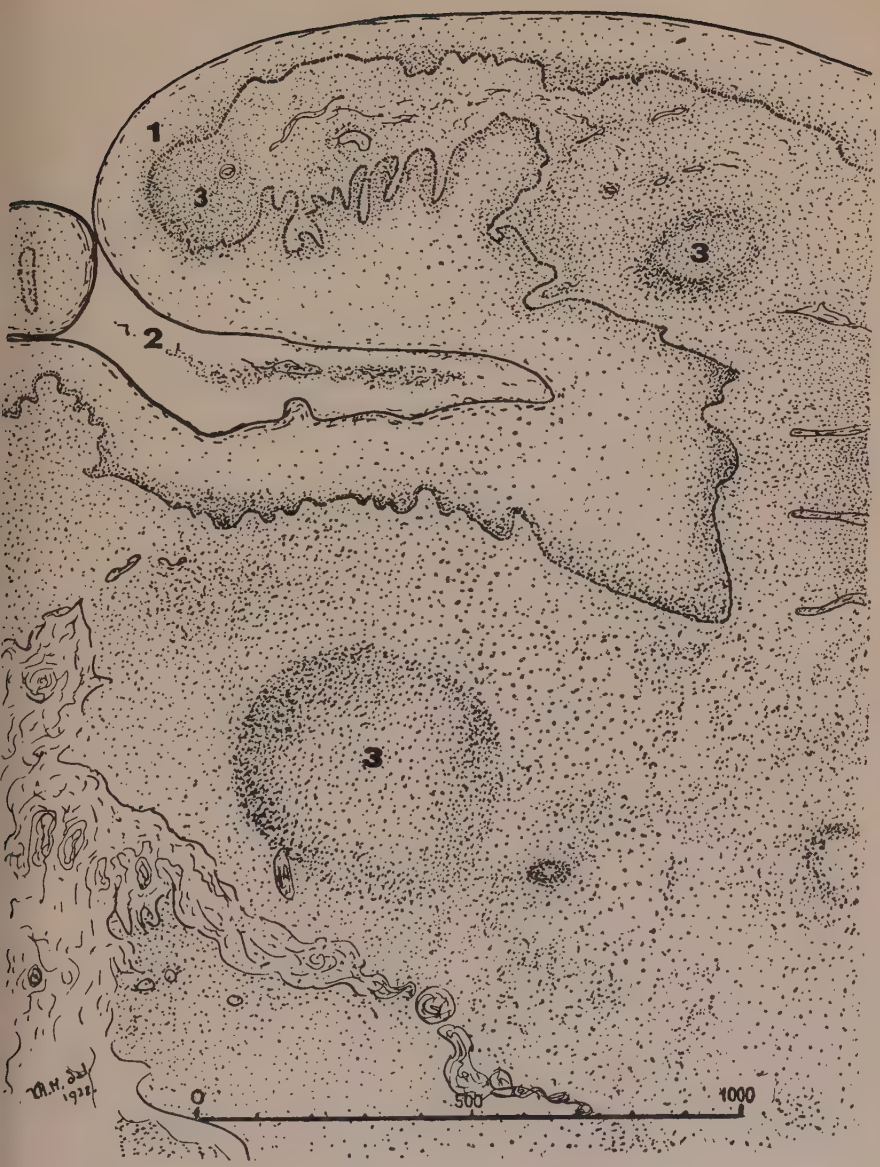



FIG. 158.—Portion of a tonsil. $\frac{2}{3}'' \times 1$. W.M.C.

1. Stratified epithelium. 2. Crypt of tonsil with epithelial debris and white corpuscles in its lumen. 3. Nodules or germ centres of lymphoid material. The tissues of the mucous membrane are infiltrated, as is also the stratified epithelium, with myriads of white corpuscles.

consists of a number of primary nodules, strung together on a strand of delicate connective tissue, and each one of these

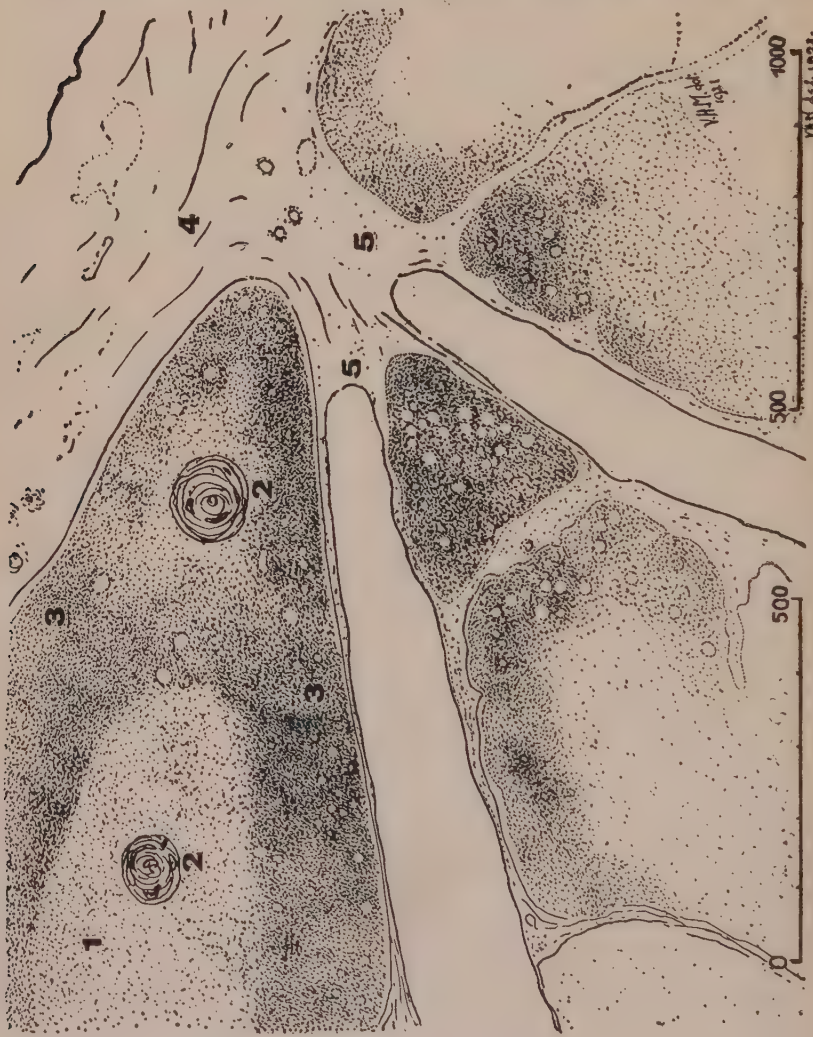



FIG. 159.—Thymus. ⅜″ × 2. G.A.H.

1. Medulla. 2, 2. Hassall's corpuscles. 3. Cortex. 4. Connective tissue capsule. 5. Trabeculæ of connective tissue dividing the gland

nodules is divided incompletely into secondary nodules which consist of a cortex and medulla. Under the microscope we see a connective tissue capsule which sends down trabeculæ

into the interior of the gland, but in man no further than the cortex (fig. 159). The partitions are rather more regular than those of the ordinary lymph gland. The pulp consists of a reticulum rather finer in the cortex than in the medulla, and in the meshes of this reticulum are found masses of lymphocytes. Again, these are more dense in the cortex than in the medulla, but in the former position they are *not* found grouped round germinal centres. The structure characteristic of the medulla is the concentric corpuscle of Hassall. This consists

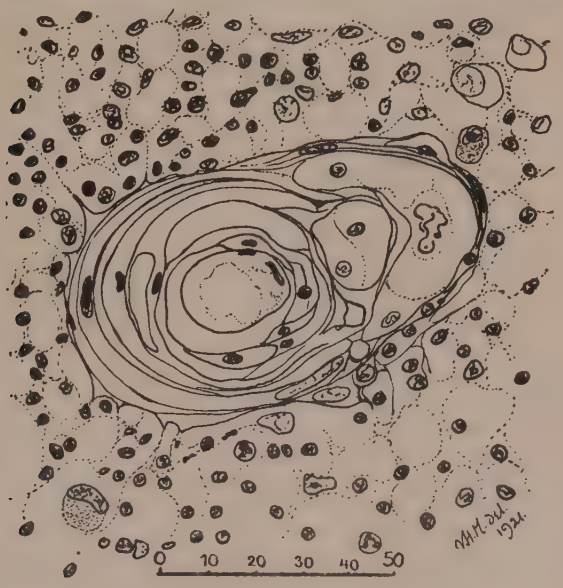



FIG. 160.—High-power view of a Hassall's corpuscle from the medulla of a thymus gland. $\frac{1}{6}''$ × 4. G.A.H.

Compare this drawing with figs. 155 and 163, in which similar structures are depicted.

of (degenerated ?) crescent-shaped cells, often swollen and of an epithelial nature, and *may* be formed from the endothelial cells of small arteries (figs. 159 and 160). The thymus rarely persists into adult life, though the original structure can always be made out in the atrophied organ. This disappearance of a lymphoid or adenoid organ like the thymus calls to mind the disappearance of the adenoid masses in the pharynx and appendix as age advances.

**Hæmolymph Glands**—In man, and other mammals, we

constantly find glands which have the general appearance of lymph glands, with the exception that there are blood sinuses in them, into which the red corpuscles of the blood penetrate freely, as well as lymph sinuses and follicles, into which they do not penetrate.

The main organ of this type is the spleen, which hitherto has been included for much the same reason as the thymus with the endocrine organs. Morphologically it is simplest to consider it as a large blood sinus or sponge (into the meshes of which blood freely penetrates) containing a system of tiny lymph follicles just visible to the naked eye, arranged on the course of the arteries of the gland (fig. 161). Over the spleen there

FIG. 161.—Hand-lens view of a section of the spleen. W.M.C.

1, 1. Artery on the branches of which are situated the Malpighian bodies. 2. A large Malpighian body. 3. A small Malpighian body.

is a thick capsule, consisting mainly of unstriped muscle (its distinguishing feature) with a small amount of white fibrous and elastic tissue (fig. 162). Portions of this capsule dip down into the body of the gland, and carry blood vessels, both arteries and veins. These strands are called, as usual, trabeculæ. At the surface they are approximately at right angles to the direction of the capsule, but more internally they branch and run in all directions. The main pulp of the spleen consists of a fine reticulum of connective tissue, continuous with the white fibrous tissue of the trabeculæ. These reticular fibres are wrapped round with connective tissue cells. In the meshes of this network are found red blood corpuscles and lymphocytes. The latter are present in greater numbers than in the blood.

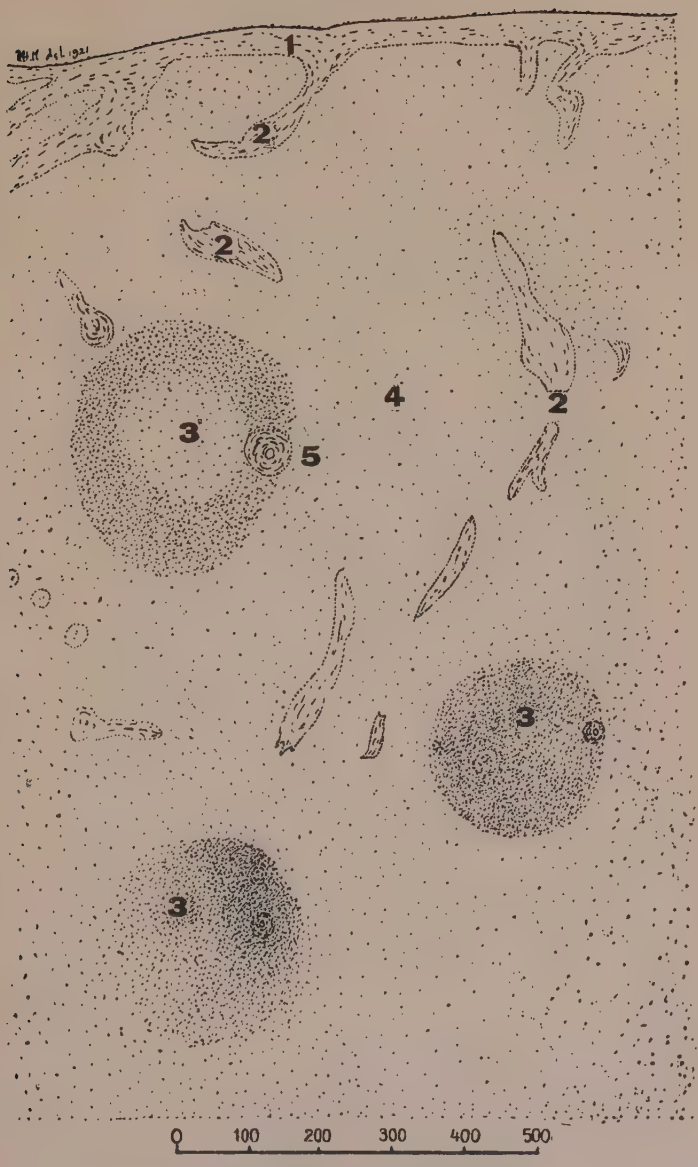



FIG. 162.—Spleen. $\frac{3}{8}$″ × 2. G.A.H.

1. Capsule consisting mainly of unstriped muscle. 2, 2. Trabeculæ extending from the capsule into the medulla of the spleen. 3, 3. Malpighian corpuscles consisting of lymphoid material, each with its artery. 4. Pulp of spleen in which red blood corpuscles are found in great numbers (see fig. 163). 5. Artery of Malpighian corpuscle.

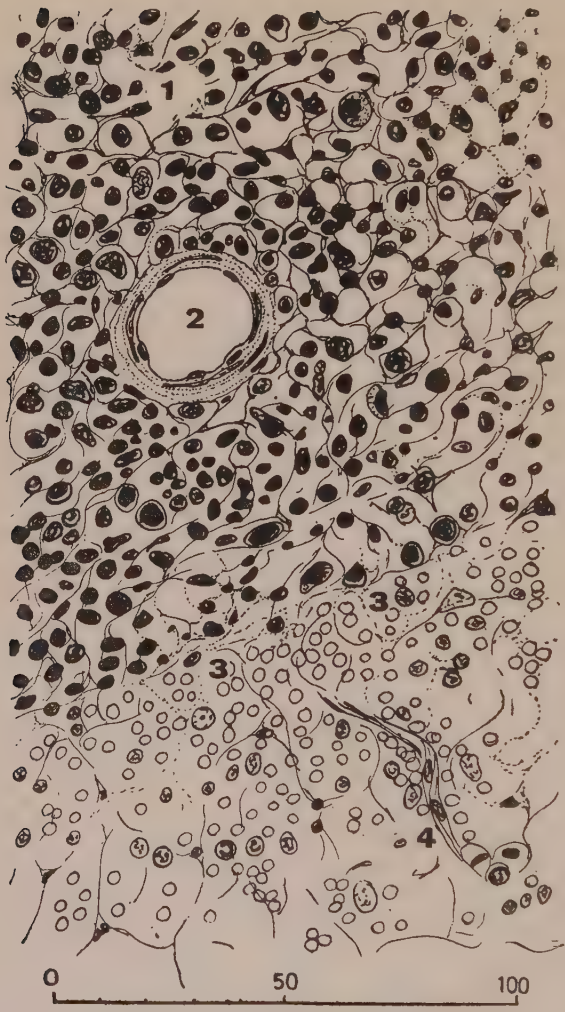



FIG. 163.—Spleen ($\frac{1}{8}$″ × 4), showing the edge of a Malpighian body and the spleen pulp below.

1. Lymphoid material of Malpighian body. The cells are mainly those of reticular tissue, with small lymphocytes in the meshes. There are one or two large lymphocytes visible. 2. Artery. 3, 3. Pulp of spleen with very numerous red corpuscles—the white circles—and a number of polymorphonuclear leucocytes in its meshes. 4. Unstriped muscle fibres of a small trabecula.

If we follow the arteries we find that they leave the trabeculæ and branch in the pulp of the spleen. Shortly after they leave the trabeculæ we find developed on their course small oval lymph follicles known as the Malpighian bodies of the spleen (figs. 161 and 162). In the outer layers of these, lymphocytes are packed more closely than in the interior, and as there is considerable mitotic activity, the cells are stained more deeply there than elsewhere. Although these Malpighian bodies are found on the course of the arteries, and although there is a considerable capillary network over them, there is *no* penetration of the blood elements into their intimate structure. Consequently the Malpighian bodies, when the section has been stained with a double stain, one of which picks out red blood corpuscles, are of an entirely different colour from the rest of the section. This is demonstrated in fig. 163, which shows the edge of a small Malpighian body in the upper part, with an artery in the centre, and at the lower edge the ordinary pulp of the spleen. It will be seen that there are no red blood corpuscles visible in the Malpighian body.

(On looking at this diagram it is easy to see how, if the artery were to degenerate and the endothelial membrane to swell, we could easily obtain an appearance like that of the Hassall's corpuscle in fig. 160.)

## CHAPTER V

# HOLLOW ORGANS

THERE is a group of organs in the body which, owing to their similar structure, we can conveniently group as hollow organs. These are the œsophagus, stomach, the whole of the alimentary canal, the trachea, bronchi and bronchioles, the bladder, the uterus and ureters, and urethra. (Logically, too, the heart and blood vessels should be included in hollow organs, but they have already been dealt with.)

A diagrammatic section of a hypothetical hollow organ is given in fig. 164. It consists of three layers. Starting from the innermost, there are : (1) the mucous coat—mucous membrane ; (2) the submucous coat ; (3) the muscular coat.

THE MUCOUS MEMBRANE—This consists of either compound epithelium, columnar or ciliated epithelium, or a glandular structure, according to the function of the organ. It may even have, as in the small intestine and Fallopian tube, large finger-like projections into the lumen of the hollow organ. The innermost coat of the mucous membrane is usually a strand of unstriped muscle, called the muscularis mucosæ.

THE SUBMUCOUS COAT—This consists of loose connective tissue. It sometimes, as in the œsophagus, duodenum and trachea, contains a few glands. The distribution of the blood vessels to the glands of the mucous membrane takes place in this coat, and consequently it is usually highly vascular.

THE MUSCLE COAT—This usually consists of two coats, an inner circular and outer longitudinal coat. The muscle is unstriped except in the œsophagus. Between the circular and longitudinal coats in the alimentary tract there is the nerve plexus of Auerbach to be seen, and upon the inner surface of the circular coat the plexus of Meissner (figs. 69, 70). The longitudinal coat is usually much the thinner.

Hollow organs, then, can be differentiated one from the other, first by the nature of the mucous membrane, second by the presence or absence of glands in the submucous coat, and

third, by the muscular coats, their number, arrangement and elementary nature. Of these, the first is by far the most important.

Taking a hand lens and examining sections of the œsophagus

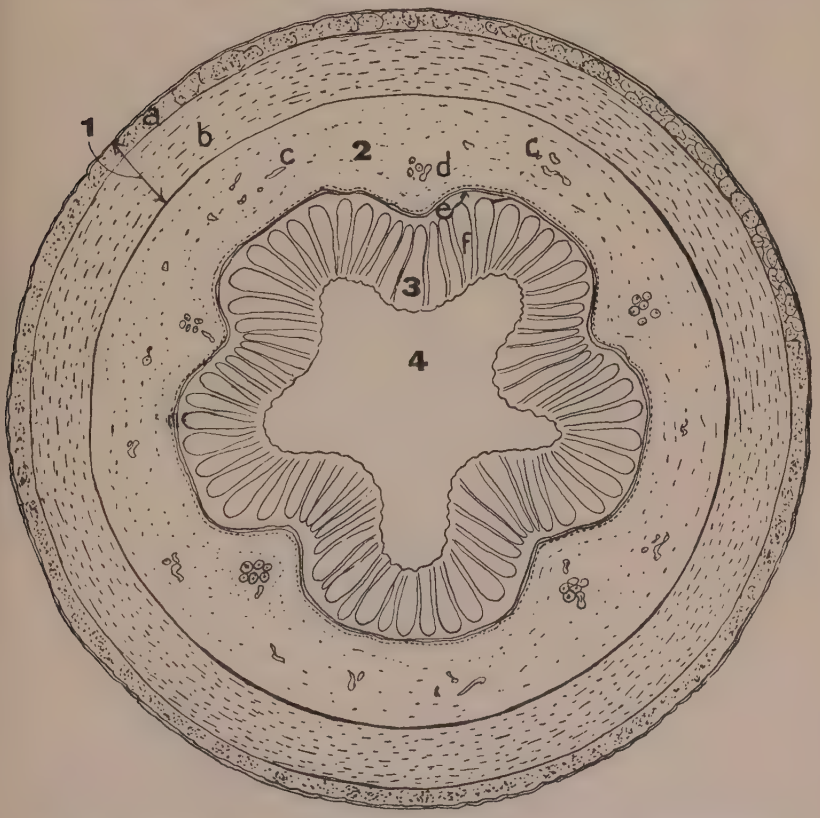



FIG. 164.—General plan upon which the structure of hollow organs is based.

1. Muscular coat. *a*. Longitudinal coat. *b*. Circular coat.
2. Submucous coat, consisting of connective tissue with blood vessels, *c*, and glands, *d*.
3. Mucous membrane. *e*. Outermost layer, the muscularis mucosæ. consisting of longitudinal and circular fibres. *f*. The glands of the mucous membrane.
4. The lumen.

(fig. 165), stomach, small intestine, uterus (fig. 166), large intestine (fig. 167), and trachea (fig. 168), we see, first, that the lumen of the organ remains completely open in the trachea only. This is due to the split ring of cartilage in its outermost coat. In the other organs the lumen is more or less closed.

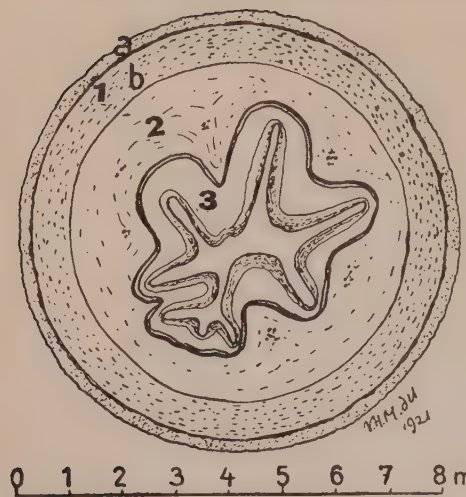



FIG. 165.—Hand-lens view of œsophagus.

1. Muscular coat. *a*. Longitudinal. *b*. Circular.
2. Submucous coat.
3. Mucous membrane with thick muscularis mucosæ and stratified epithelium.

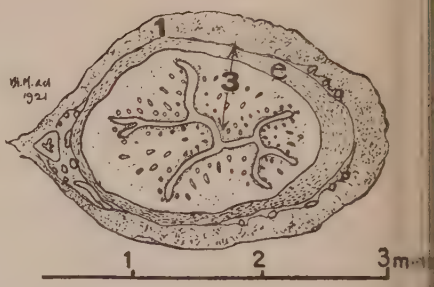



FIG. 166.—Hand-lens view of uterus.

1. Muscular coat.
3. Mucous membrane with, *e*, enormously thick m... cularis mucosæ—mainly circular.

Note the second, or submucous, coat is thin and sho... chiefly by the blood vessels between the circular m... cularis mucosæ and the (mainly) longitudinal muscu... coat.

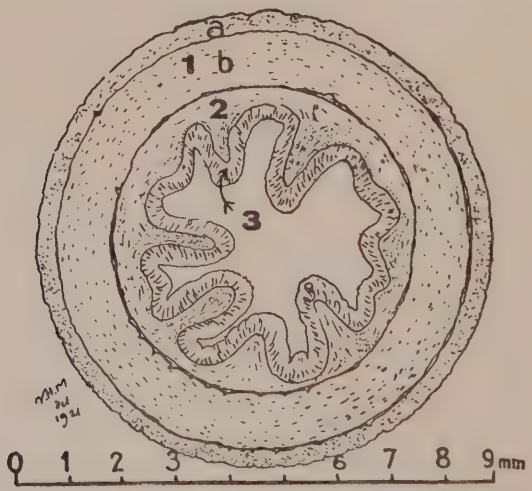



FIG. 167.—Hand-lens view of large intestine.

1. Muscular coat. *a*. Longitudinal. *b*. Circular.
2. Submucous coat.
3. Mucous membrane.

Note.—The muscular coats are very thick in the large intestine.

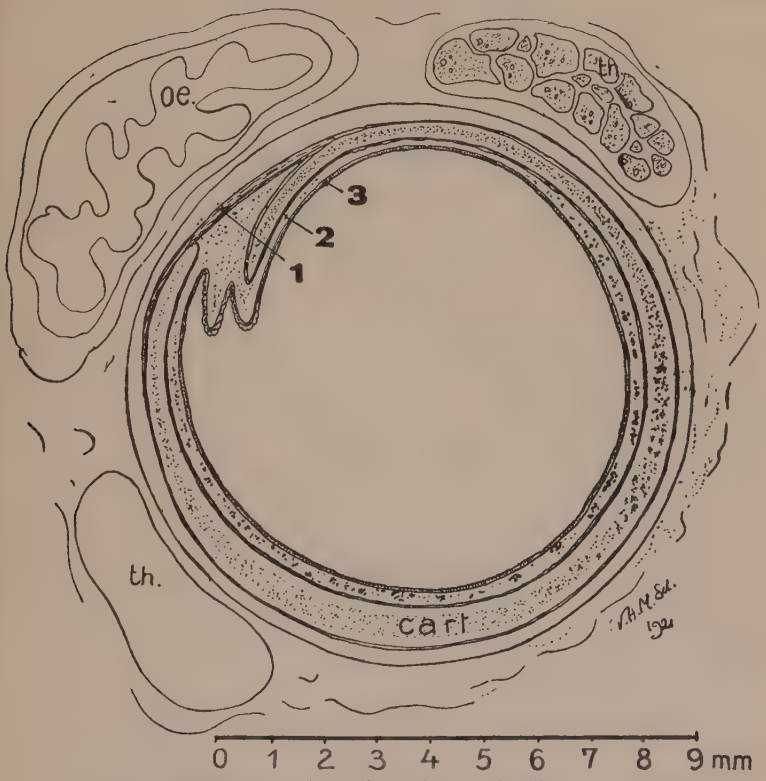



FIG. 168.—Hand-lens view of trachea and adjacent structures.

1. Muscle uniting the ends of the split ring of cartilage.
2. Submucous coat.
3. Mucous membrane.
*œ.* Œsophagus. *th.* Thyroid. *cart.* Cartilage.

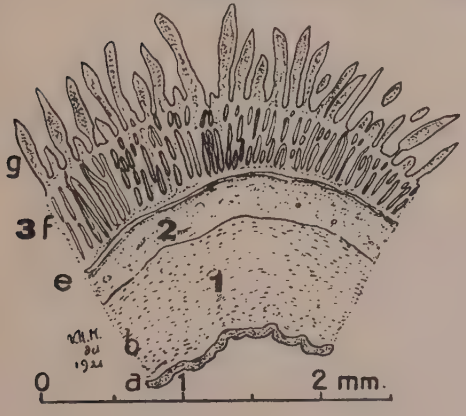



FIG. 169.—Hand-lens view of small intestine.

1. Muscular coat. *a.* Longitudinal muscle coat. *b.* Circular coat.
2. Submucous coat.
3. Mucous membrane. *e.* Muscularis mucosæ. *f.* Glands or crypts of Lieberkühn. *g.* Villi projecting into the lumen of intestine.

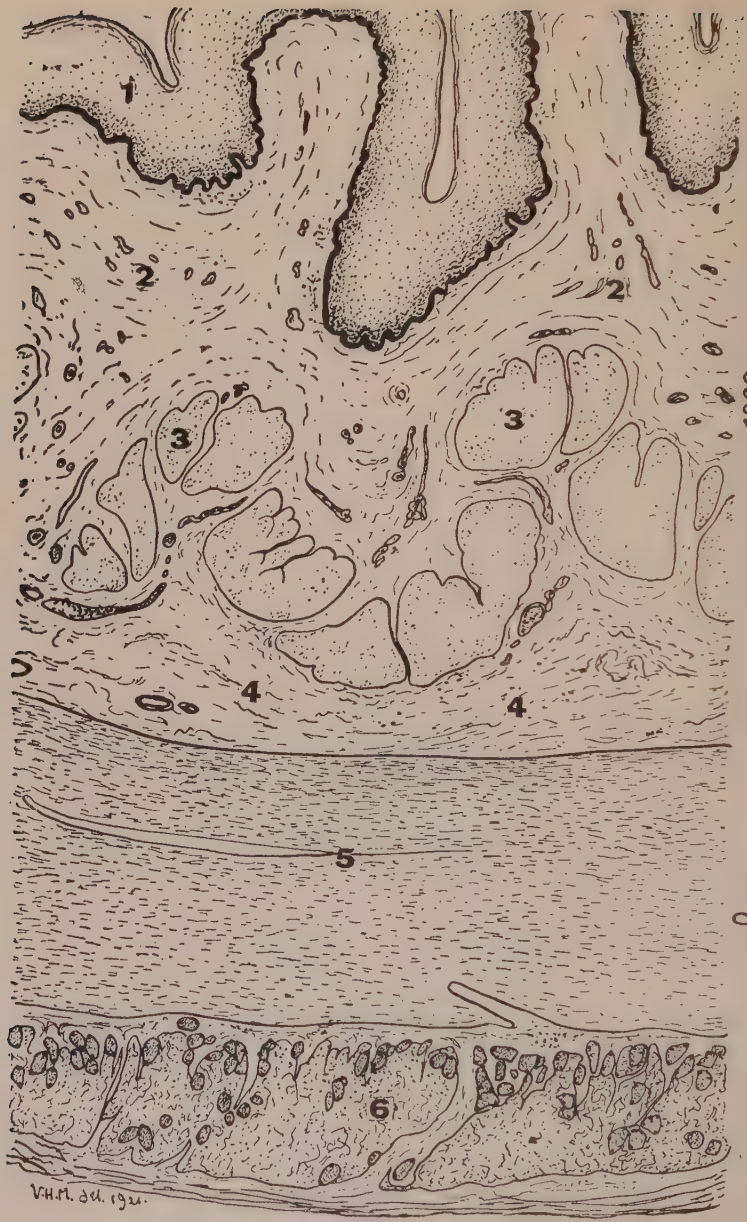



FIG. 170.—Œsophagus. $\frac{3}{8}$″ × 1. K.C.W.

1. Stratified epithelium. 2, 2. Glands and their ducts. 3, 3. Muscularis mucosæ. 4, 4. Submucous coat containing glands. 5. Circular muscle coat. 6. Longitudinal muscle coat with many striped muscle fibres among the unstriped (the darkly shaded areas are striped muscle).

This is markedly so in the œsophagus and the uterus, and to a less extent in the large intestine. This should mark these organs off from the rest. In the small intestine (fig. 169) there are small finger-like projections into the lumen of the organ which distinguish it from every other organ, except the Fallopian tube. The thickness of the muscle wall is some guide, though not a very reliable one, for at the pyloric end of

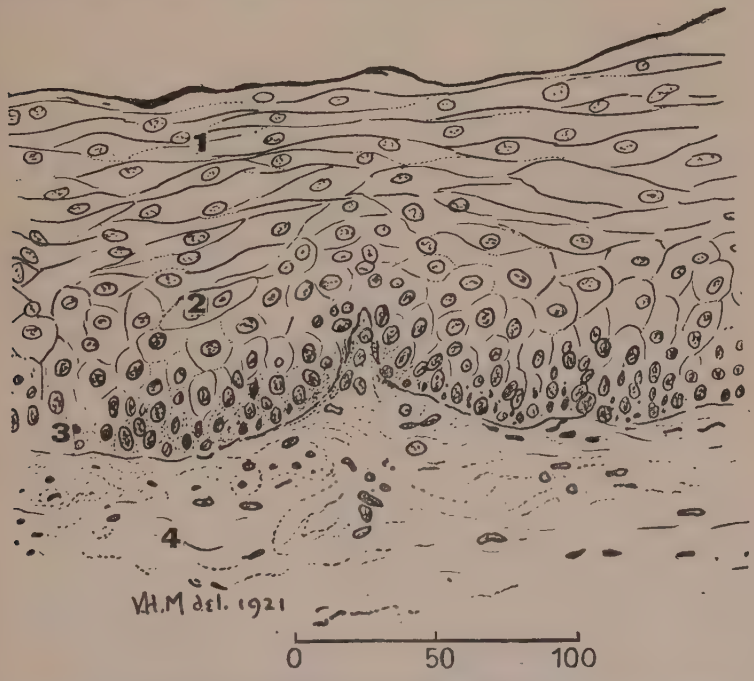



FIG. 171.—Stratified epithelium of œsophagus. $\frac{1}{6}$″ × 2. C.

1. Superficial layers of cells with flattened, poorly staining nuclei. 2. Deeper layers, consisting of polygonal cells with well-staining nuclei. 3. Deepest layer of immature cells with deeply staining nuclei. 4. Connective tissue of mucous membrane.

the stomach, the large intestine and the uterus, the muscle walls are thick. It will be convenient to take the various organs we have mentioned in order and discuss the distinguishing features of each.

**The Œsophagus**—The distinguishing features of the œsophagus are, first, the mucous membrane, which consists externally of a stratified epithelium (fig. 171). (The only other organs which *might* be confused with it on this ground

are the ureter, bladder and vagina, where the epithelium is a compound epithelium with four or five cells superimposed, in the œsophagus there are approximately twenty.) Secondly, there is a large development of the muscularis mucosæ[1] (see fig. 170), and this should distinguish it from every other organ but the uterus, the greater part of whose walls can be considered to be hypertrophied muscularis mucosæ. Thirdly, the

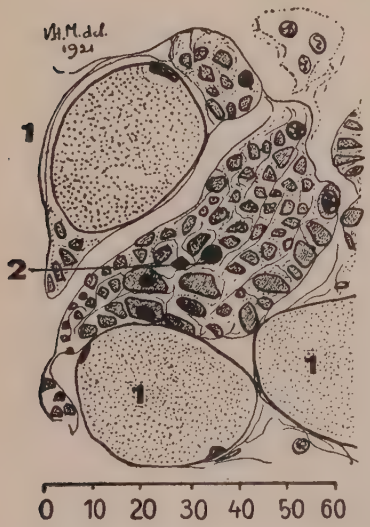



FIG. 172.—Muscle of the longitudinal coat of the upper end of the œsophagus. $\frac{1}{8}'' \times 4$. K.C.W.

1. Transverse section of striped fibres (note position of nuclei and the size of the fibre).
2. Unstriped muscle fibres, a few of which are cut through their nuclei.

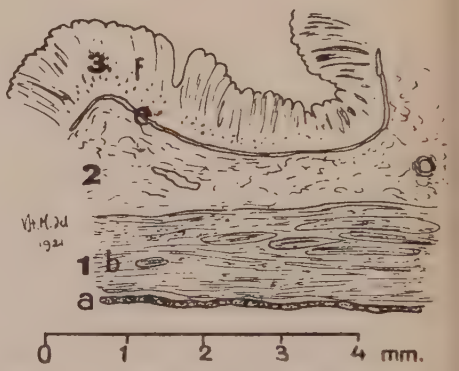



FIG. 173.—Hand-lens view of cardiac end of stomach in transverse section.

1. Muscular coat. *a*. Longitudinal. *b*. Circular.
2. Submucous coat.
3. Mucous membrane. *e*. Muscularis mucosæ. *f*. Glands.

submucous coat contains a few scattered glands, the œsophageal glands (see fig. 98). Fourthly, the outer longitudinal muscle contains striped muscle as well as unstriped muscle. In fig. 170 this is a characteristic feature. The darkly stained oval triangular areas are striped muscle, whereas the remainder consists of unstriped muscle. The high-power view of a small portion of this coat is given in fig. 172. It shows the two sorts of muscle in transverse section. It should be noted that striped muscle is found usually in only the upper two-thirds

[1] Human beings and dogs.

of the œsophagus, but in some animals it extends throughout the whole length.

**The Stomach**—In the stomach the arrangement is typical of a hollow organ, the distinguishing feature being the mucous membrane, which is different according to the end of the stomach to which it belongs. At the cardiac end we find glands with chief and oxyntic cells, as described above; at the pyloric end, tubules containing one type of cell only (figs. 91–93 and 95–97). There is some extension in both

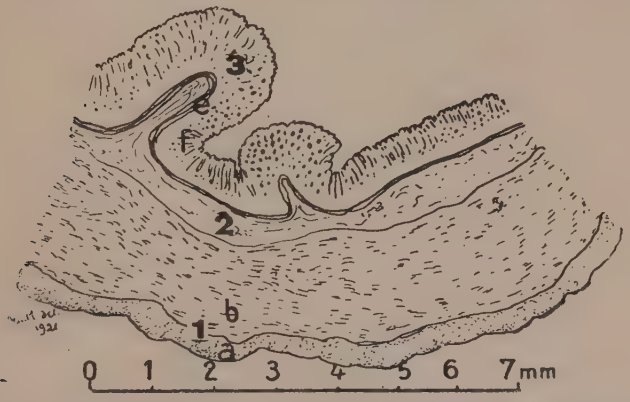



FIG. 174.—Hand-lens view of the pyloric end of the stomach.
1. Muscular coat. *a*. Longitudinal. *b*. Circular.
2. Submucous coat.
3. Mucous membrane. *e*. Muscularis mycosæ. *f*. Glands.

parts of the muscle fibres of the muscularis mucosæ up between the glands (figs. 92, 95, 96), and this is most obvious in the pyloric end of the stomach, but is an uncertain guide. The chief method of distinction is the presence or absence of the characteristic oxyntic cells. For the hand-lens appearance of the stomach walls at the cardiac and pyloric ends respectively, see figs. 173 and 174.

**The Small Intestine**—Again, in the small intestine it is the mucous membrane that is the distinguishing feature, although in the upper portion we do find Brunner's glands in the submucous coat, which are an additional distinctive feature. The mucous coat consists of two parts: (1) finger-like projections (a millimetre, or 1,000$\mu$ long) into the intestine, and (2) the secretory glands, the crypts of Lieberkühn. A general view of the villi can be obtained from the figs. 169 and 175. (See also villi of the Fallopian tubes.)

FIG. 175.—Villi of the mucous membrane of the small intestine. $\frac{2}{3}''$ × 4. W.M.C.

1. Columnar epithelium. 2. Reticular connective tissue of the villi. 3. Unstriped muscle. 4. Villus cut obliquely.

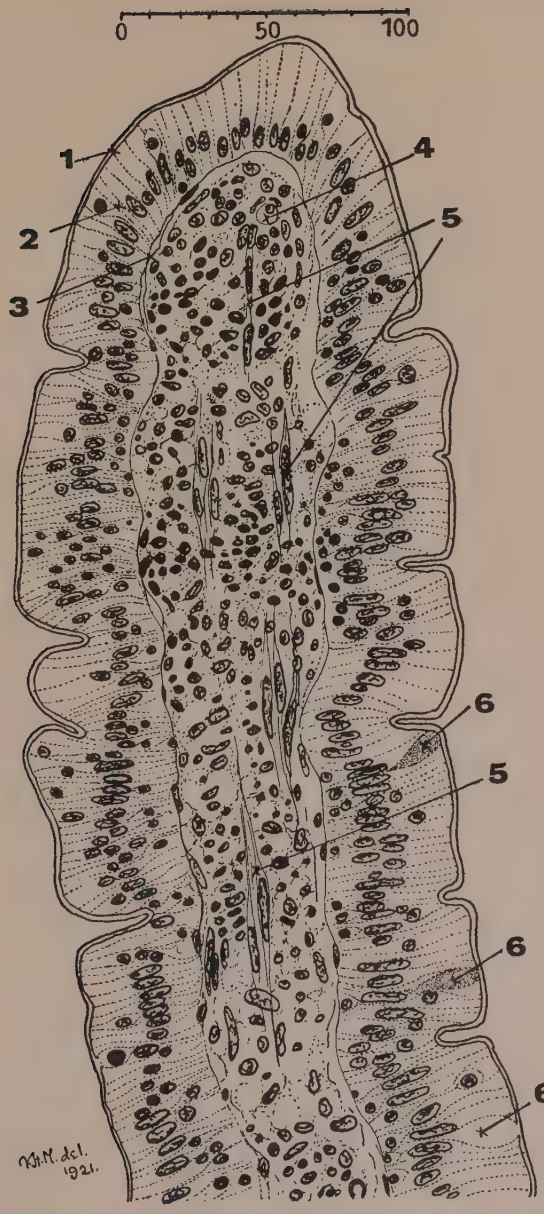



FIG. 176.—Portion of villus of small intestine. $\frac{1}{8}'' \times 2$. W.M.C.

1. Striated border of epithelium.
2. Columnar epithelium.
3. Basement membrane.
4. Capillary.
5, 5. Unstriped muscle.
6, 6, 6. Mucous or goblet cells.

A villus is coated with columnar epithelium, some 40$\mu$ tall, with long narrow cells containing oval to rod-shaped nuclei. Here and there goblet cells are visible (fig. 176). Beneath the epithelium there is a basement membrane of connective tissue. Internally there is a reticular connective tissue, in the meshes of which there are found leucocytes. Immediately under the basement membrane capillaries are

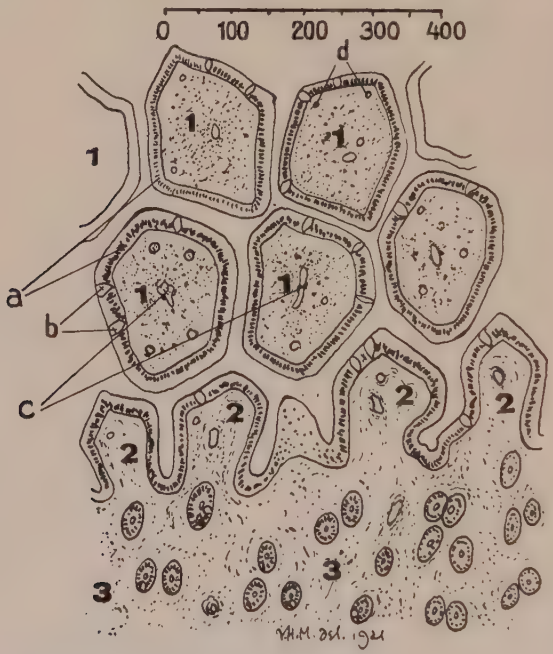



FIG. 177.—Mucous membrane of small intestine cut obliquely so that villi and crypts of Lieberkühn are seen in transverse section. $\frac{2}{3}''$ × 2. K.C.W.

1, 1, 1, 1. Villi. *a*. Columnar epithelium. *b*. Goblet cell. *c*. Central lacteal. *d*. Capillaries.
2, 2, 2, 2. Lower ends or necks of villi, showing columnar epithelium and lacteals.
3, 3. Mucous membrane proper, with many crypts of Lieberkühn.

found. There is a rich blood supply to the villi. Centrally placed there is a lymph vessel (best seen in transverse section: see fig. 177), the lacteal, and running vertically throughout the length of the villus are unstriped muscle fibres well shown in the high-power diagram (fig. 176). Often a villus has a crinkled appearance which may be reasonably ascribed to contraction of the unstriped muscle in the process of fixation. This unstriped muscle passes on down and joins the muscularis

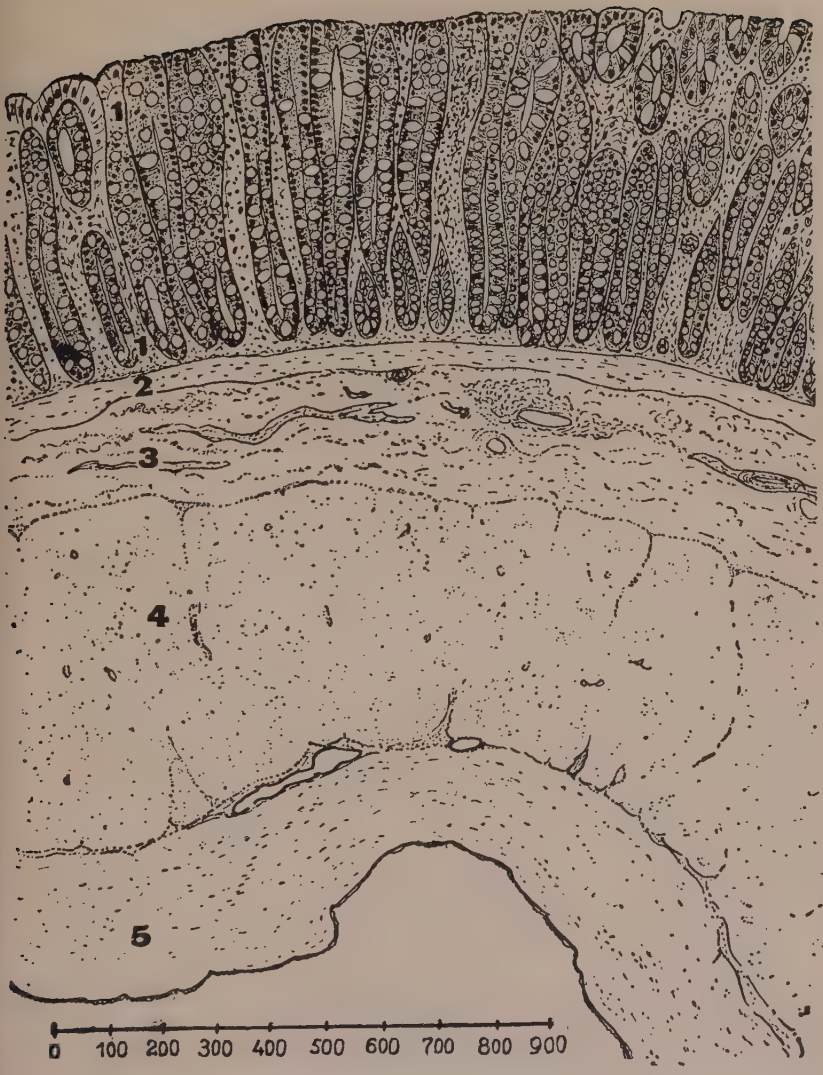



FIG. 178.—Large intestine.

1. Mucous membrane with simple tubular glands containing many mucous cells (showing as clear oval areas). 2. Muscularis mucosæ. 3. Submucous coat with many blood vessels. 4. Circular muscle. 5. Longitudinal muscle coat.

mucosæ. The crypts of Lieberkühn have already received description above (fig. 94 and page 109).

**Large Intestine**—The large intestine is comparable on the one hand with the stomach, and on the other with the uterus (fig. 178). The distinction between them is best based on the mucous membrane. It is true that the mucous membrane of the stomach superficially resembles the mucous membrane of the large intestine; but the glands are closely set together in the large intestine, they are not so long, they have more obvious lumina, and the mucous cells, being such striking phenomena, easily distinguish it from the stomach. On the other hand, the large intestine bears a superficial resemblance to the **uterus.** The muscle walls are thick, and, in the lower animals, arranged in exactly the same order. But closer inspection reveals marked differences (fig. 179). In the first place, the mucous membrane is unlike that of the large intestine. It is thick and spongy, and very vascular. It is beset with glands, which, however, are not as closely placed to each other as they are in the large intestine. Moreover, these glands are not straight, but wavy, and at the lower end sometimes branched. Consequently a section will pass through glands cut at different levels. The cells which line the glands are columnar and ciliate, indeed the whole mucous membrane is covered with columnar ciliate epithelium. (As is usual, these cilia are not conspicuous in a laboratory preparation, unless special precaution has been taken to preserve them.) In between the glands is a ground substance beset with multitudinous spindle-shaped or irregular cells, and there are very few true connective tissue cells seen.

Immediately beneath this mucous membrane is a thick layer of circular muscle. On analogy with other hollow organs this layer must be the muscularis mucosæ, immensely hypertrophied. It is to be noted, however, that the fibres in animals with bi-cornuate uteri are mainly circular and not longitudinal, as they appear in the œsophagus (fig. 170). Farther towards the exterior, we meet with a submucous coat, in which are numerous large blood vessels, more numerous and larger, even, than in the large intestine. Internal and external to these blood vessels are found longitudinal unstriped muscle fibre bundles. The ones internal are few and more scattered, whereas the external ones are many and closely packed.

The account given above refers more to the bi-cornuate

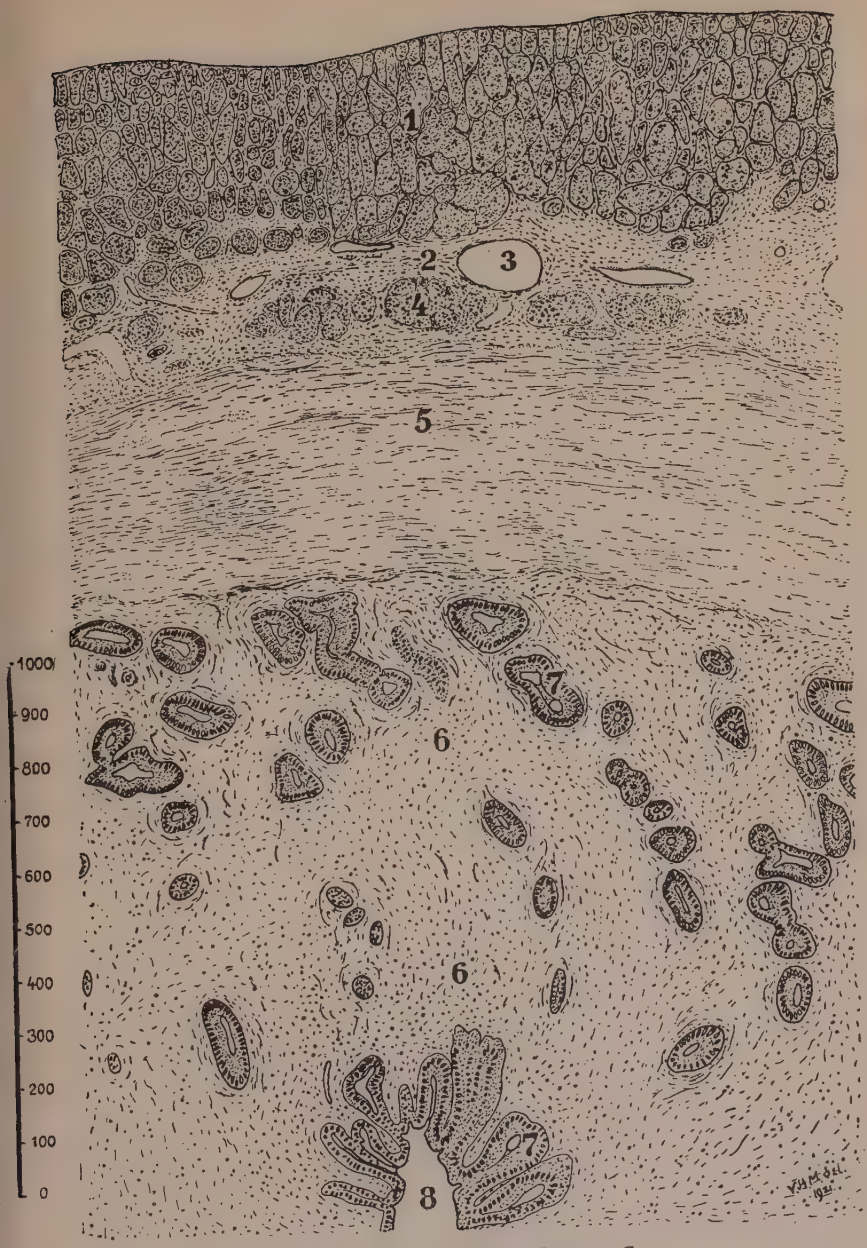



FIG. 179.—Uterus (dog). $\frac{3}{4}'' \times 1$. C.

1. External muscular coat, consisting of bundles of fibres longitudinally arranged. 2. Submucous coat, containing many large blood vessels. 3. Vein. 4. Longitudinal muscle bundle belonging to inner muscular coat. 5. Circular muscle fibres of inner muscular coat (? muscularis mucosæ). 6, 6. Connective tissue of mucous membrane. 7, 7. Glands of mucous membrane. 8. Lumen of uterus.

uteri of animals rather than to the human uterus. In it the muscle bundles are much more confused in their direction, as would be expected in view of their function in expelling the contents from a pear-shaped hollow organ.

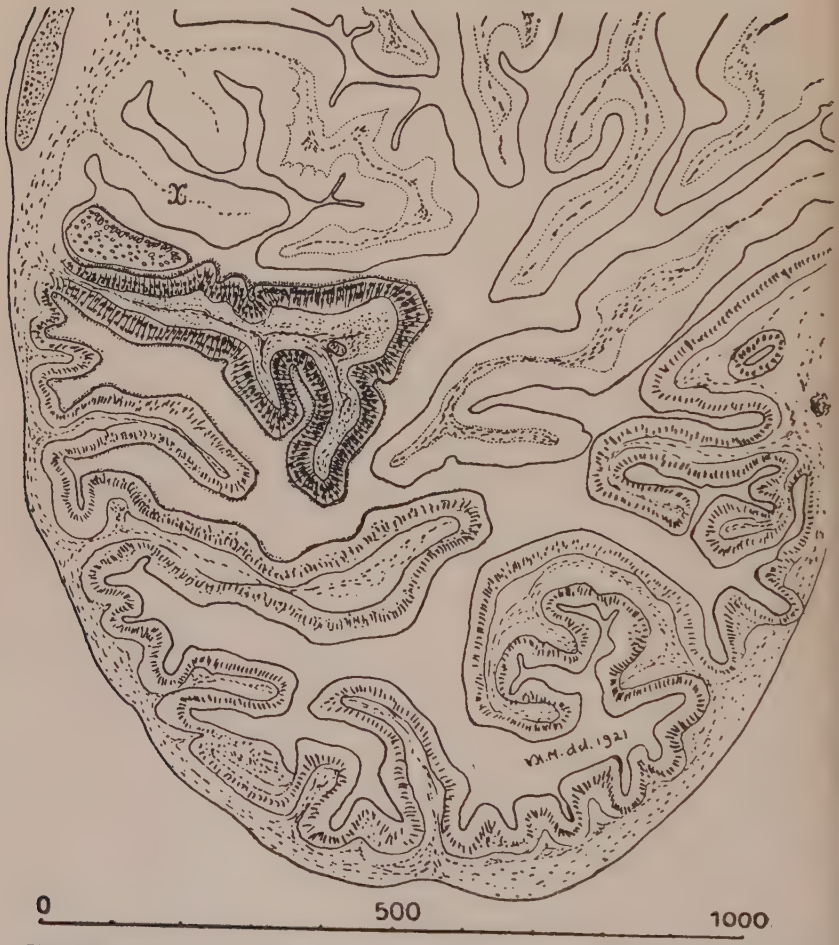



FIG. 180.—Part of a Fallopian tube showing the characteristic irregular villi. $\frac{3}{4}$" × 2. G.A.H.

**The Fallopian Tube**—A hollow organ, which might conceivably be mistaken on account of its villi, with the small intestine, is the Fallopian tube. The villi, however, are usually branched or possess irregular outlines (fig. 180), but

even the simple villi of the Fallopian tube, of which there are a few, can be readily distinguished from those of the small intestine (fig. 181). The epithelium is ciliate, the cells are somewhat broader. Internally, the amount of connective tissue in a Fallopian tube villus is small. It even appears in some parts as if the two walls of ciliated epithelium were placed on a single basement membrane (see fig. 22). There is no such development of lymphoid, muscular and vascular tissue as there is in the villus of the small intestine.

**The Ureter**—The ureter appears at first sight like the œsophagus, in that it has a compound epithelium and a lumen that is not circular, but collapsed. The distinguishing features are : (1) the mucous membrane, and (2) the layers of muscle fibres.

The mucous membrane is covered internally with a layer of transitional epithelium, four to five cells deep (fig. 182). In this it is like the bladder, and unlike the œsophagus, where there are many more cells. The cells nearest the lumen are cubical when the ureter is relaxed, and flattened when distended. Beneath this epithelium is a thick layer of connective tissue of the usual areolar type. Externally it grows coarser, and there is no distinction between submucous and mucous coats. Nor is there any muscularis mucosæ to mark the transition from one to the other (cp. œsophagus). The muscular coat is arranged in three layers (compare all other viscera), the order being: longitudinal, circular, longitudinal. The layers are not sharply differentiated one from the other, and are considerably broken up by connective tissue (cp. on the one hand the bladder, and on the other the œsophagus and other viscera). In fig. 182 the longitudinal fibres are seen to run in discrete fasciculi or bundles, and the circular layer only has the compactness seen in other viscera.

The outermost layers of the ureters consist of loose but strong connective tissue, reminiscent of the tunica adventitia of arteries and veins, and receiving the same name.

**The Bladder**—The general arrangement of the bladder follows that of the other hollow organs. The mucous membrane is lined internally with transitional epithelium (see figs. 24 and 183). Below this is a small amount of connective tissue, and there is *no* muscularis mucosæ. Often the mucous coat is wrinkled as the result of the collapse of the organ ; when it is distended the mucous membrane is flat. The submucous coat consists of rather loose areolar tissue, together with elastic fibres. There is, at times, developed a layer of

FIG. 181.—Simple villus (marked $\varkappa$ in fig. 170) of Fallopian tube under high magnification. $\frac{1}{8}''$ × 2. G.A.H.

1. Ciliated columnar epithelium. 2. Connective tissue of mucous membrane extending into villus. 3. Circular muscle coat.

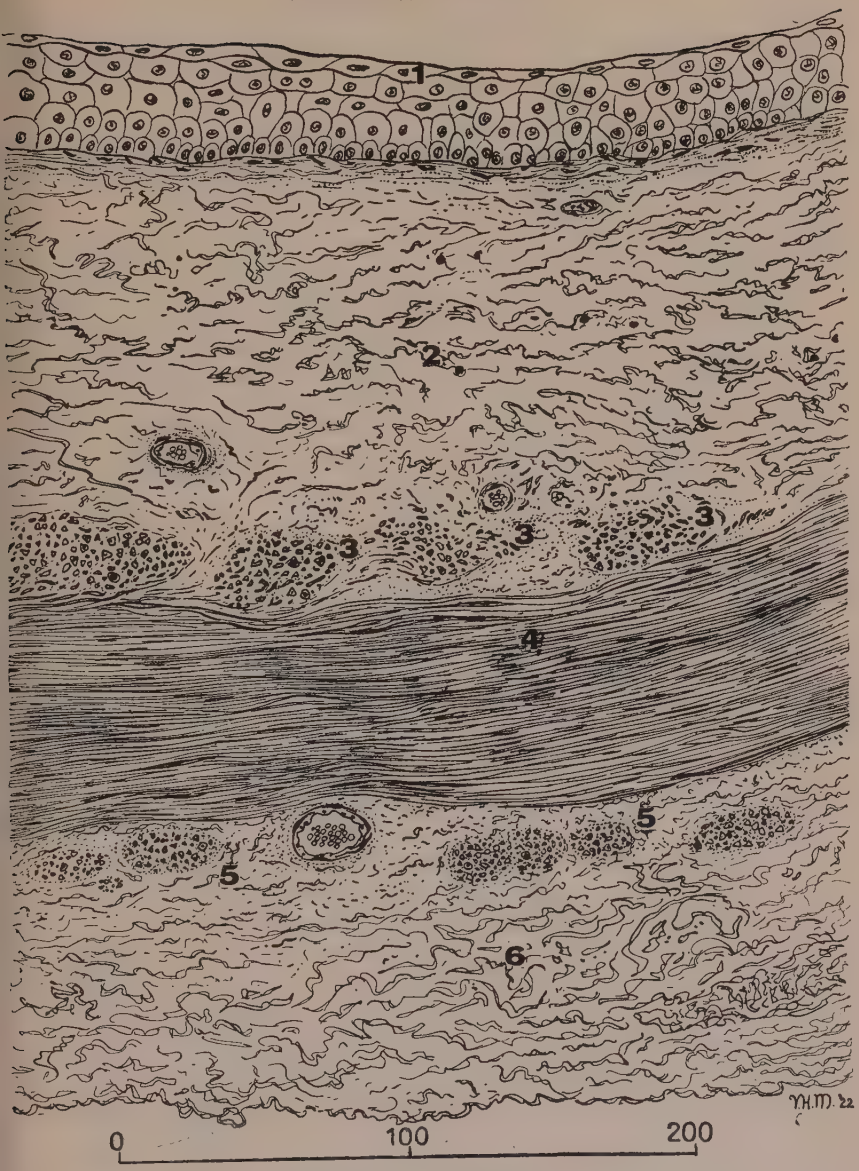



FIG. 182.—Ureter in transverse section. $\frac{1}{8}$" × 2. W.M.C.

1. Transitional epithelium. 2. Submucous coat. 3, 3, 3. Longitudinal bundles of unstriped muscle. 4. Circular coat of unstriped muscle. 5, 5. Outer longitudinal bundles of unstriped muscle. 6. Connective tissue sheath of ureter. (Note the *three* layers of muscle in juxtaposition and their order.)

unstriped muscle, and, as usual in the submucous coat, there are numerous blood vessels. When we come to the muscle coat it is difficult to discover either longitudinal or circular muscle fibre coats, although such have been described. The muscular tissue is broken up into very numerous bundles by fine connective tissue, and some of the bundles run in a more circular direction, and others, especially the outer ones, in a more longitudinal direction (fig. 183). This arrangement of muscle fibres is to be expected in a pear-shaped hollow organ which has to contract till its internal volume is zero. The things that characterize the bladder are, then, the transitional epithelium lining it, and the arrangement, or lack of arrangement, of the unstriped muscle fibres in the muscle coat.

**The Trachea, Bronchi, and Bronchioles**—In the trachea, bronchi, and bronchioles there is a considerable modification of the plan upon which hollow organs are based. The lumina in these organs have to remain patent, whereas, in the preceding organs we have described, the lumina, at some time or other in their history, have to be shut. Consequently we should expect—what actually occurs—that the muscle coat will be cut down to a minimum, and that a semi-rigid stiffening material would take its place.

**The Trachea**—The usual three coats are found (figs. 168, 184, 185). Internally the mucous membrane consists of (*a*) ciliated epithelium, upon (*b*) a basement membrane, under which is found connective tissue containing a large number of longitudinal bands of elastic tissue (see fig. 185), and a considerable number of leucocytes. There is also in this region a number of small blood vessels. The submucous coat is made up of loose connective tissue, in the meshes of which are seen numerous glands, whose ducts penetrate up to the surface through the mucous membrane (see fig. 185), together with numerous blood vessels and a small amount of adipose tissue. The third coat is characterized by an incomplete ring of cartilage, the split in the ring being posterior. Stretching across the gap in between the ends of the cartilage is: (1) connective tissue, and (2) a band of circularly arranged unstriped muscle fibres inserted into the perichondrium of the cartilage.[1] This band of muscle is the sole homologue of the muscle coat in the other hollow organs.

[1] In most animals, including human beings, the muscle is inserted into the external side of the cartilage.

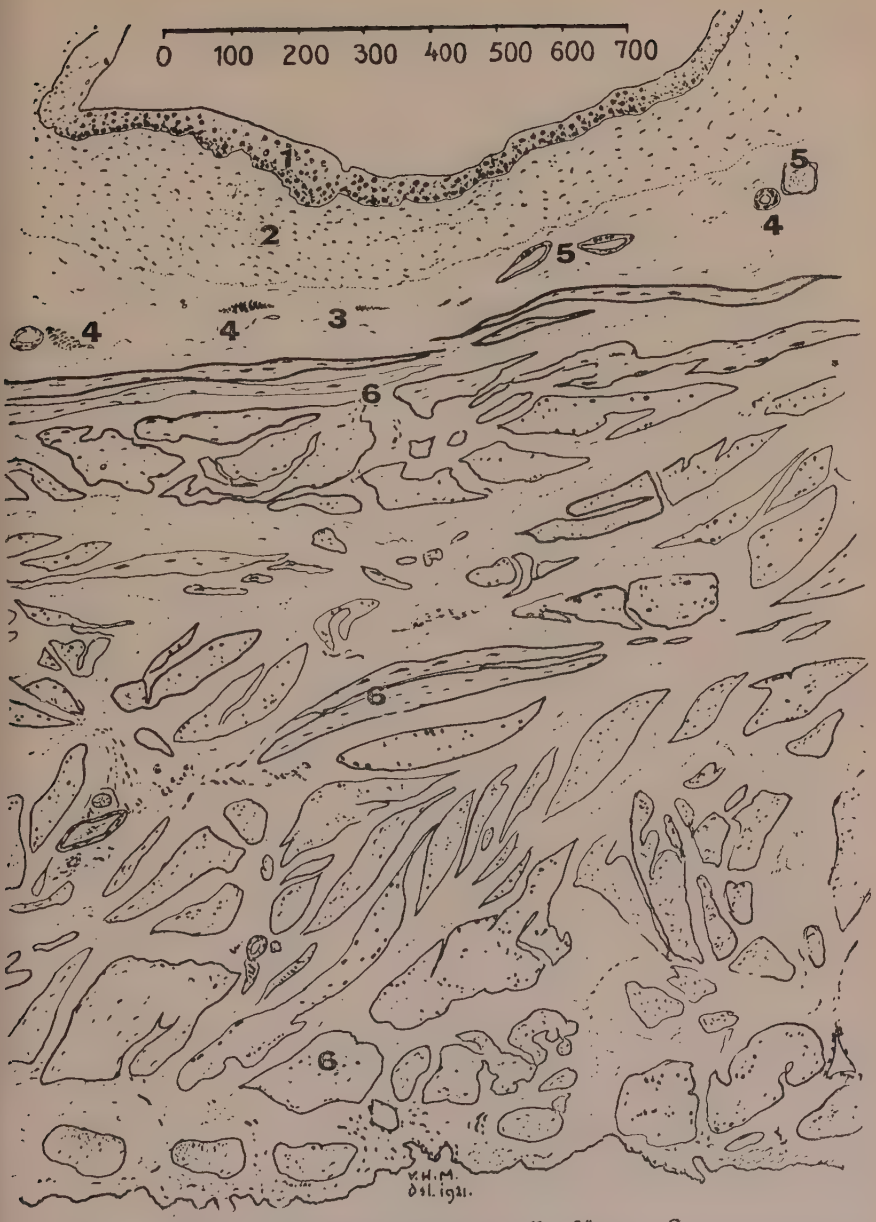



FIG. 183.—Section of bladder wall. $\frac{3}{8}$″ × 2. C.

1. Transitional epithelium. 2. Connective tissue of mucous membrane. 3. Submucous coat, with many blood vessels. 4, 4, 4. Arteries. 5, 5. Veins. 6, 6, 6. Muscular coat with many bundles of unstriped muscle, some cut longitudinally, others obliquely, and still others transversely.

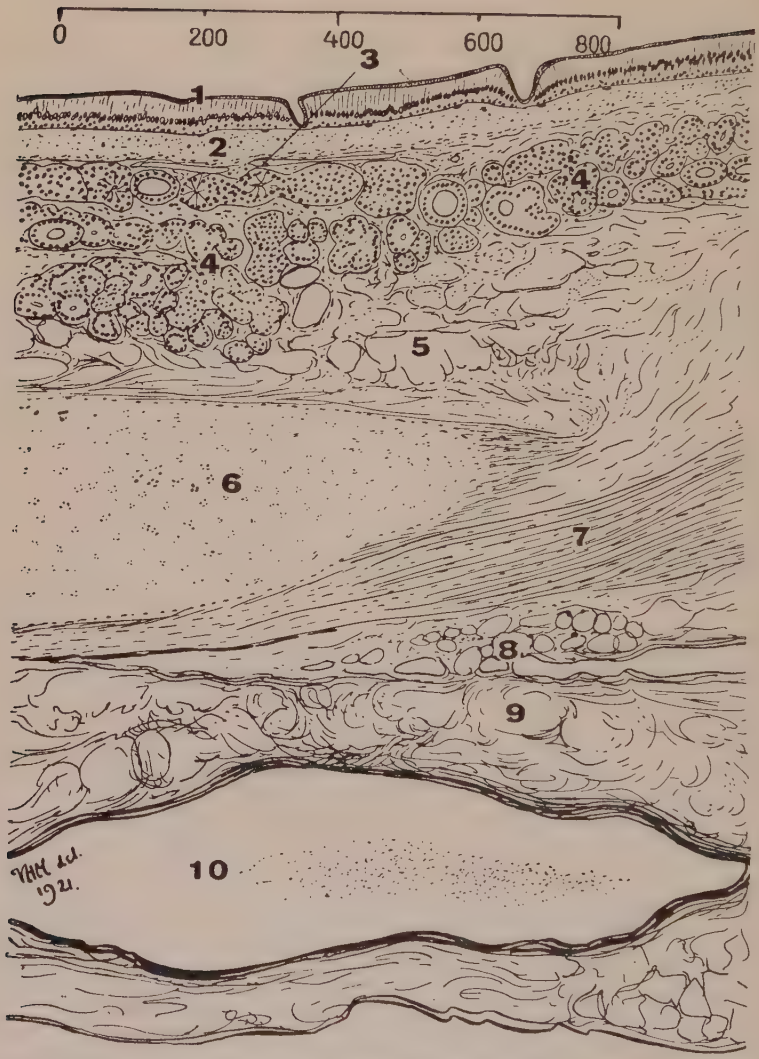



FIG. 184.—Part of a transverse section of the trachea. $\frac{3}{5}'' \times 2$. G.A.H.

1. Ciliated epithelium. 2. Connective tissue of mucous membrane, containing much elastic materia and many leucocytes. 3. Blood vessels of mucous membrane. 4. Mucous glands in submucous coat. 5. Loose connective tissue of submucous coat. 6. Hyaline cartilage. 7. Unstriped muscle bundle, connecting the two ends of the cartilage. 8. Adipose tissue. 9. Loose connective tissue. 10. Vein with debris of red blood corpuscles.

FIG. 185.—Trachea. $\frac{1}{8}'' \times 2$. G.A.H.

The section passes through the duct of a mucous tubulo-racemose gland in the tracheal wall. 1. Ciliated epithelium. 2. Elastic tissue. 3. Duct of gland. 4. Vein with debris of red blood corpuscles. 5. Alveoli of glands cut tangentially. 6. Alveoli cut transversely. 7. Cartilage.

**The Bronchi and Bronchioles**—These are arranged very similarly to the trachea. The smaller branches of the bronchi, the bronchioles, contain rings of cartilage incomplete in three or four places. Again the gap is bridged by muscle. The gaps in the rings now bear no relation to the lie of the lungs, otherwise the appearance of the bronchi is very closely similar to that of the trachea. When we come to the small bronchioles we find that the cartilage entirely disappears and the bronchiole (see figs. 186 and 115) now consists of: (1) a ciliated epithelium standing upon a basement membrane, beneath

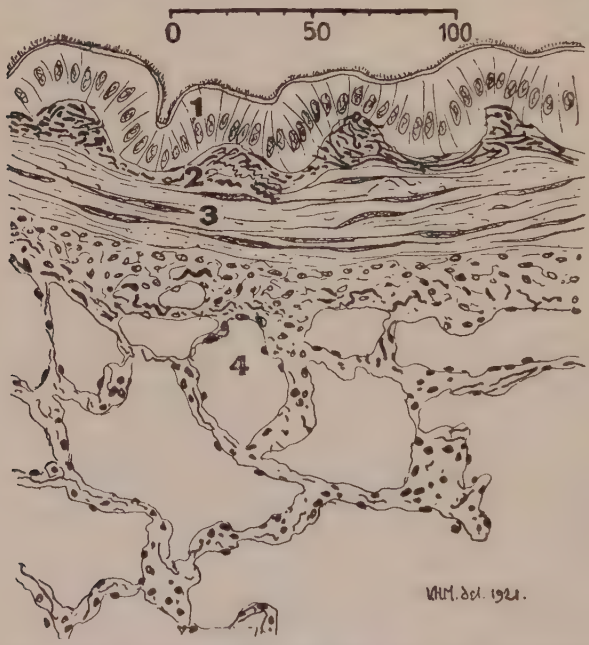



FIG. 186.—High-power drawing of a part of the wall of a bronchiole. $\frac{1}{6}''$ × 2. G.A.H.

1. Ciliated epithelium. 2. Elastic material of mucous membrane. 3. Circular muscle coat. 4. Lung tissue.

which is developed a large amount of elastic fibres, and this tissue, which represents the mucous membrane, is in close juxtaposition to a circular band of unstriped muscle, which goes completely round the small bronchiole. Immediately external to this is connective tissue which passes at once into the reticular tissue of the alveoli of the lungs.

## CHAPTER VI

# THE SKIN AND SKIN APPENDAGES

COVERING the whole of the body, and continuous with the mucous membrane of the orifices of the body, is the skin, a structure consisting of a superficial layer, the epidermis, cuticle or scarf skin, and a deeper connective tissue membrane, highly vascular and of considerable thickness, the cutis vera (true skin), or corium. Its function is threefold: (1) to present a relatively tough, impervious coating towards the world; (2) to regulate the temperature of the body; and (3) to present a sentient surface to the play of stimuli from a changing environment. The outer surface of the skin is, therefore, composed of keratinized epithelial cells as already described (p. 26). The thickness of this layer depends much on the position of the body from which it arises. On the abdomen (fig. 187) it is relatively thin; on the sole of the foot (fig. 188) it is thick. This is a natural result of the kind of wear and tear to which the skin in these positions is exposed.

The epithelium of the skin is stratified. The innermost layer consists of columnar to cubical cells, affixed by denticulations to the outermost layer of the corium or true skin. The cells have distinct, sharply and deeply staining nuclei. It is in this layer that karyokinetic figures are to be found, for continual division is taking place to fill the place of cells in the outer layers which are shed owing to wear and tear. The epithelium is continually renewing itself from inwards outwards. The innermost layer is not straight, but wavy (fig. 187). It will often extend deeply down into the cutis vera. The portions of corium (cutis vera) in between are spoken of as papillæ. (This characteristic of invading the true skin is of importance in considering the enamel organ of teeth and the structure of hairs.)

The cells budded off from the innermost layer of the

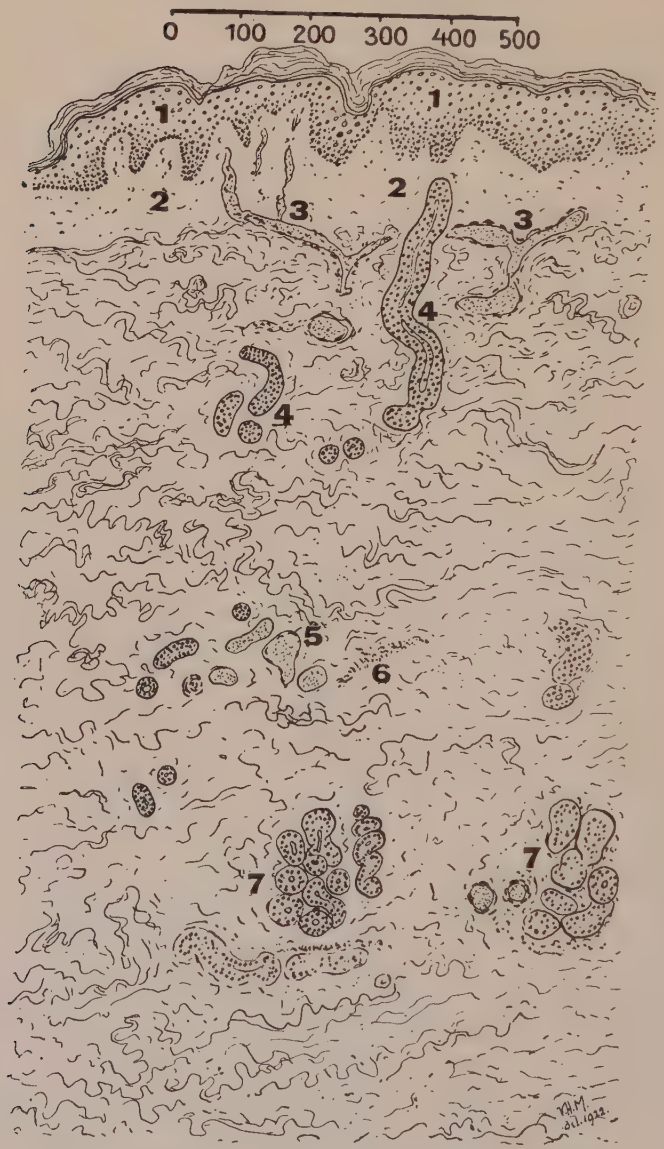



FIG. 187.—Skin of abdomen (human). $\frac{3}{8}$″ × 2. K.C.W.

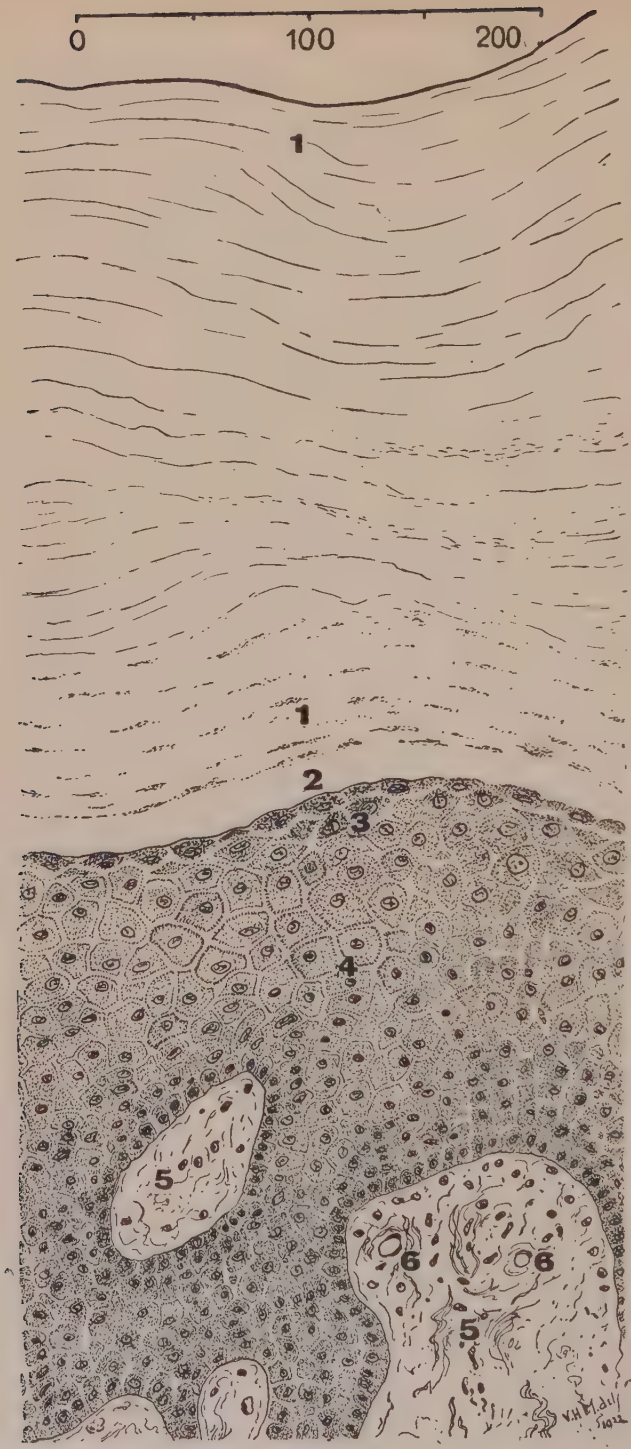
1, 1. Stratified epithelium of skin, showing, externally, scaly layers of stratum corneum, then the stratum lucidum, and, more deeply, the rete mucosum. 2, 2. True skin (cutis vera). 3, 3. Small blood vessels. 4, 4. Ducts of sweat glands. 5. Group of veins. 6. Artery cut tangentially and longitudinally. 7, 7. Sweat glands.

epithelium assume polyhedral forms, and, as explained before, do not fit directly on to their neighbours, but are connected to them by fine processes of protoplasm, giving rise to the appearance of "prickle cells" (fig. 188). As we leave the deeper layers we find the cells becoming more lozenge-shaped and granular. The epithelium from the deepest layer to this point is termed the Malpighian layer or rete mucosum. (This is the pigmented layer in dark-skinned races.) In the next layer the cells are granular, and these granules stain very readily with hæmatoxylin or carmine. This stratum (the stratum granulosum) is thickest in the soles of the foot, and inconspicuous where the epidermis is thin (cp. figs. 187 and 188). Directly outside the granular layer we meet a clear, translucent layer, in which the cell outlines and granules are invisible. This layer is called the stratum lucidum. Beyond this the cells become more and more flattened, the nuclei are invisible and the cell outlines difficult to see. Ultimately cells are hard, flattened, horny, and scale-like, and are continually desquamated. This external layer, the thickness of which varies according to the position of the body, is called the stratum corneum, or horny layer.

The keratinized cells of the stratum corneum become resistant to physical agencies (thorns, stones, etc.), and also to chemical agents. This is particularly so when there is an active production of sebaceous material. Cold concentrated sulphuric acid may run over the hand without doing much damage as long as it is rapidly washed off in a powerful stream of cold water. Alkalis and hot water, however, make the skin less resistant, both by getting rid of the sebaceous material and by softening the horny layer.

Beneath, and protected by the epidermis or cuticle, is the cutis vera, or true skin, which, on tanning, forms leather. It is a thick, highly vascular and sentient layer, consisting of a dense interwoven fabric of connective-tissue bundles. More deeply, the bundles are coarser and looser. Every papilla has its tuft of capillaries, and, among other things, the function of these vessels is to supply nutrient material to the rapidly growing epithelium immediately above and around it. (Another function is that of maintaining the body at a constant temperature, see below.)

Often, in these papillæ, sensory apparatus is seen (see fig. 194). Elastic fibres are found throughout the cutis vera,




1, 1. Thick layer, consisting of flattened cells, the stratum corneum.

2. Stratum lucidum.

3. Stratum granulosum.

4. Rete mucosum of Malpighi, showing prickle cells.

5, 5. Papillæ of true skin, or cutis vera : the one to the left appearing as an island because it is cut tangentially to its tip.

6, 6. Capillaries.

FIG. 188.—Skin of toe (human). $\frac{1}{8}'' \times 1$. K.C.W.

finer in the papillæ, and coarser in the deeper layers. In the latter position they are arranged parallel to the surface. The amount varies very much according to the position in the body. As might be expected, there is a considerable development of elastic tissue in the skin of the abdomen. Muscle fibres (unstriped) are found wherever hairs are developed in the skin, and also in the scrotum, penis, perineum, and nipples.

The inner margin of the cutis vera is difficult to determine, for the latter passes insensibly into the subcutaneous tissue. The fibrous material becomes more and more loose and open, there is a considerable admixture of adipose tissue, and the coiled-up tubes of the sweat glands appear. Beneath these we may be said to be in subcutaneous tissue.

The blood vessels, in addition to their nutritive function, help to regulate the heat of the body, by radiating heat in smaller or greater amounts. Further, the fat aids in heat retention, as does the hair. (The latter is also a protection against weather and attack.)

**Hairs**—These are appendages of the skin, useful (1) in maintaining the heat of the body, (2) as sensory apparatus, and (3) as decoration. The structure of the hair and its root can best be understood if we imagine the Malpighian layer (the rete mucosum) dipping down through the cutis vera into the subcutaneous tissue and there forming a specialized papilla (see fig. 189). The growing point of this papilla gives rise to a peculiar epithelial structure which, on increasing in length, pierces the epithelial layers above it, and emerges on the surface as a hair.

The hair, then, has two portions, its root and its shaft: the root is firmly planted in a recess formed by the epithelium's dipping down through the cutis vera, often into subcutaneous tissue, and the shaft, continuous with the root, projecting above the surface of the skin. Except in the eyelids (eyelashes) the root (and therefore the shaft) slopes. And there is an arrangement of the roots on a definite pattern, special to the individual, but general to the species.

Fig. 189 is a diagrammatic representation of a hair follicle (the epithelial recess in which the hair grows), together with the lower portion of a hair. The stratified epithelium is continuous with the lining of the follicle, the outer root-sheath, but the number of cells is very much reduced, and the stratum corneum does not extend beyond the mouth. At the mouth

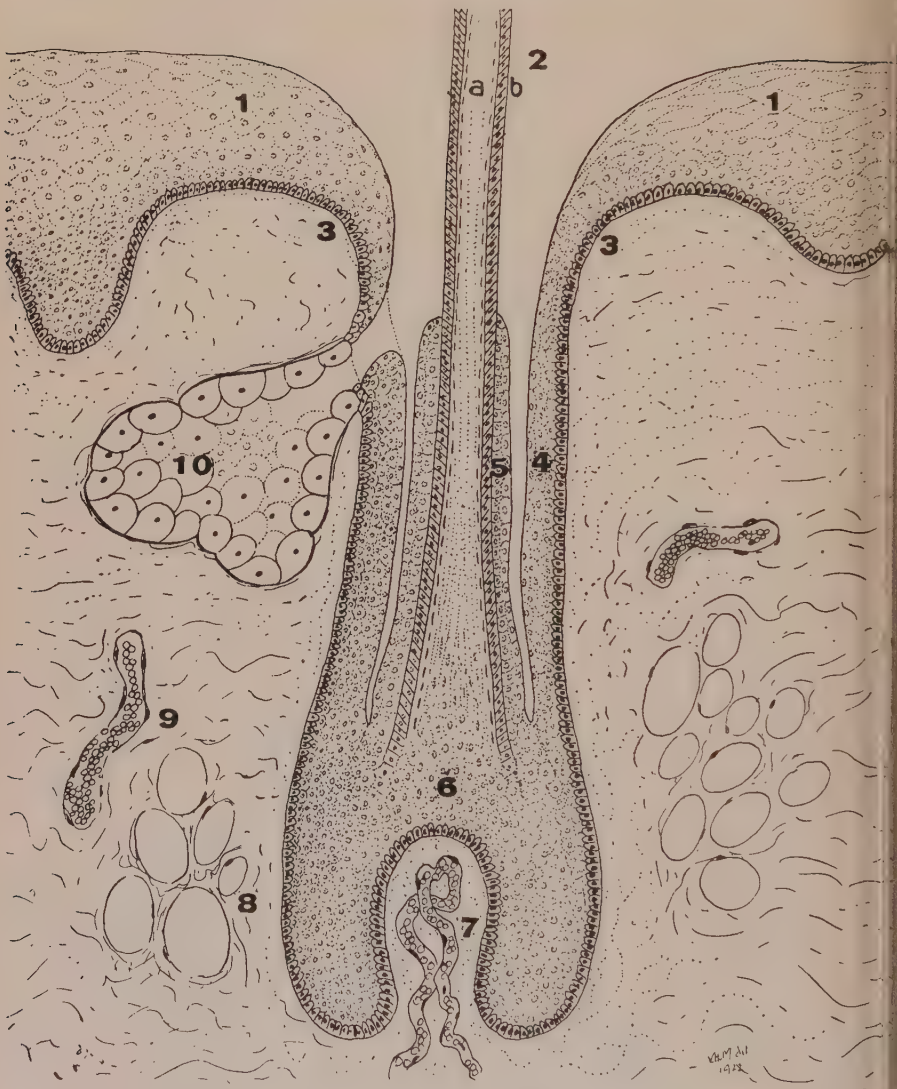



FIG. 189.—Hair-root and root-sheath (diagram).

1, 1. Stratified epithelium. 2. Hair: (*a*) medulla, (*b*) cuticle. 3. Innermost layer of the rete mucosum. 4. Outer root-sheath. 5. Inner root-sheath. 6. Growing-point of hair. 7. Papilla of hair, with capillary. 8. Fat cells of subcutaneous tissue. 9. Capillary of subcutaneous tissue. 10. Sebaceous gland opening out into root-sheath.

the outer root-sheath is pierced by the mouth of a sebaceous gland (see also fig. 140). Near the lower end of the follicle the epithelium returns on itself, forming the inner root-sheath, consisting of two layers of cells, Henle's and Huxley's layers respectively. This passes outwards, ensheathing the hair as far as the mouth of the hair follicle, where it stops short. At the extreme end of the root the epithelium evaginates to form the papilla of the hair, which is crowned by actively dividing cells. These, as they grow upwards, differentiate and form the different layers of the hair : (1) the scaly covering, or hair cuticle ; (2) the fibrous or cortical substance, consisting of long, flattened, fusiform cells, forming longitudinal fibres ; and (3) the medulla, absent in the fine hairs of the body, consisting of dried cells with air-particles in between. The pigment of the hair is found in the fibrous layer. Into the papilla of the hair, blood capillaries penetrate, and are important in supplying the growing-point of the hair with nutriment. Over the lower portion of the follicle is the *dermic* coat, consisting of thin firm layers of connective tissue, containing many elastic fibres.

In some animals there are specialized hairs (the "whiskers," sinus or tactile hairs), which are encased in an additional development, a blood-sinus, between the inner and outer layers of the dermic coat. Otherwise their structure is the same. Fig. 190 shows two such hairs cut obliquely, and several developing hairs. Attached to the hair follicles can generally be found strands of unstriped muscle. These pass down obliquely from the surface of the skin to the lower ends of the sheaths, and serve the purpose of altering the inclination of the hairs. They are the so-called pilomotor muscles, and, when contracted, cause the ruffling of hair seen in fear, anger, or cold. In addition, nerves pass to the hair follicles, and their axis cylinders end either in a plexus around the outer root-sheath or in plaque endings in the outer layers of the outer root-sheath.

**Teeth** — Another mechanism, the shape of which is moulded by an invagination of the stratified epithelium, is the teeth. Teeth may be prepared for investigation under the microscope in the same way as bones and for the same reasons. Fig. 191 gives a drawing of a ground-down section of a tooth, and fig. 192 of a decalcified tooth in its socket in the jaw.

FIG. 190.—Section showing two types of hairs, erectile and normal, in early stage of development. $\frac{3}{8}'' \times 2$. W.M.C.

1. Hair, cut obliquely, just piercing the skin, showing cuticle and medulla. The inner root-sheath can be traced some way down. 2. Superficial layers of stratified epithelium. 3. Deeper layers, or rete mucosum, continuous with outer root-sheath. 4, 4, 4. Developing hairs. 5, 5. Sheaths containing sinuses of erectile hairs. 6. Root of an erectile hair cut obliquely. 7. Unstriped muscle bundles.

A tooth may be considered as consisting of three portions: the crown, projecting above the gum; the root, securely fixed in a socket or alveolus of the jaw; and the intermediate portion, the neck. The socket into which the roots are fixed is lined with dense connective tissue, continuous with the connective tissue and stratified epithelium of the gums (fig. 192). All teeth are hollow (fig. 191). The root (fang) is pierced at the lower end, and through this hole run blood vessels and nerves to the closed cavity, the pulp cavity, within the tooth. The pulp of the pulp cavity contains a jelly-like connective tissue, blood vessels, nerves, and connective-tissue cells. The latter are collected more particularly near the surface of the pulp cavity under the body of the tooth. In developing teeth they are columnar, but when the tooth is fully formed are flattened. They are called odontoblasts (cp. osteoblasts) and send fine fibrils into the substance of the tooth.

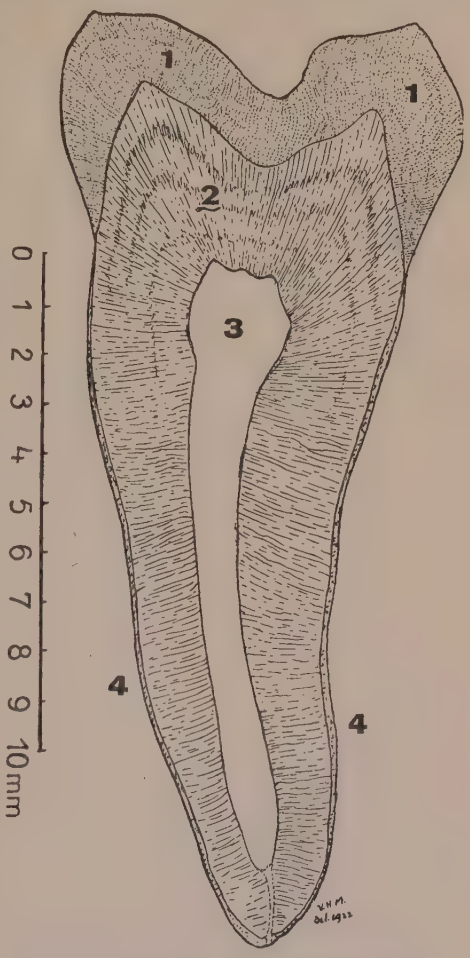



FIG. 191.—Section of a tooth ground dry. × 6·4. P.C.E.

1. Adamant or enamel. 2. Ivory or dentine. 3. Pulp cavity. 4, 4. Substantia ossea or cement substance.

The body of the tooth is seen to consist of two layers. In the crown we meet, externally in the adamant or enamel, the hardest and most mineral part of the body: 3·5 per cent.

only of it is animal matter. This is found on the exposed surface of the crown. It may be worn down by continual use. On the cutting edge it is thickest, and then thins down towards the neck, where it ceases. The adamant is deposited by the adamant organ (see later), an ingrowth of the epithelium of the mouth, and as the vigour of the adamant organ varies

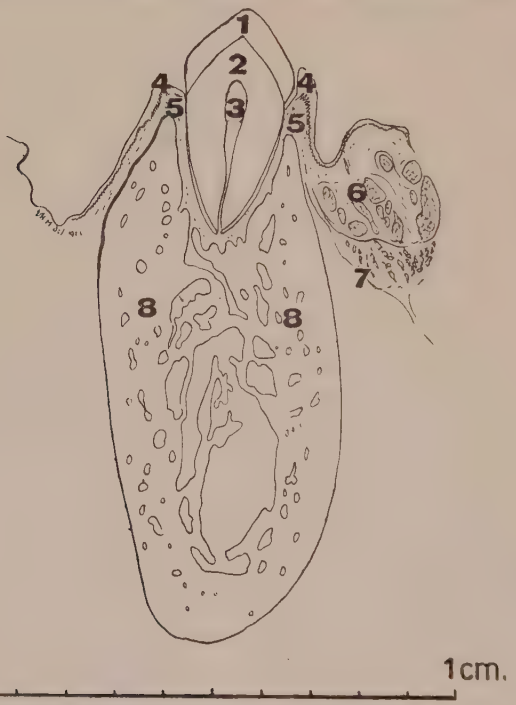



FIG. 192.—Section of a tooth *in situ*. Hand-lens view. × 6·4. P.C.E.

1. Adamant or enamel of tooth. 2. Ivory or dentine. 3. Pulp cavity. 4, 4. Stratified epithelium of buccal mucous membrane. 5, 5. Connective tissue lining socket of tooth and continuous with the true skin of the buccal mucous membrane. 6. Salivary gland. 7. Striped muscle in transverse section. 8, 8. Bone of jaw.

from time to time, the enamel shows striation parallel to the surface. Whatever depresses the activity of the adamant organ (disease, lack of calcium and vitamin) affects the deposition of adamant. The enamel is striated radially too, for it is composed of hexagonal prisms, with parallel sides, but not necessarily straight.

From the point where the adamant leaves off, i.e. at the neck of the tooth, to the end of the root, the tooth is covered extern-

ally by the substantia ossea, cement substance, or crusta petrosa. This consists of a layer of tissue, thicker around the apices of the fangs and their grooves, which looks like true bone under the microscope. There are lamellæ, lacunæ, and canaliculi similar to those in bone, and where the cement is very thick there may be Haversian canals. The cement substance is covered by a dental periosteum.

The main part of the tooth (crown as well as root) is formed of ivory or dentine. This is a substance somewhat like bone, but having a different structure under the microscope. The groundwork consists of a gelatine-yielding animal tissue (28 per cent.), in which is deposited calcium phosphate and carbonate, together with magnesium phosphate, to the remaining 72 per cent. The ivory is permeated by narrow tubules running radially out from the pulp cavity towards the external adamant or substantia ossea. These tubules are approximately parallel, and so give the dentine a striated appearance. They open out into the pulp cavity at one end, and at the other terminate by free ends. There are side branches which make anastomoses with the neighbouring tubules. Into these tubules (which are homologous with the canaliculi of bone) pass protoplastic processes of the odontoblasts and possibly nerve fibrils.

**Development of Teeth**—To understand this it is best to consider a papilla of a stratified epithelium and corium and imagine it ossified. The Malpighian layer of the epidermis deposits the enamel externally and shapes the tooth; the connective-tissue corpuscles of the corium (becoming odontoblasts) deposit the ivory internally. The stages are as follow: (*a*) The epithelium of the buccal cavity thickens and there is a downgrowth of it, in a strand, into the tissues of the primitive jaw. This strand, the dental lamina, divides into two plates, one vertical and the other horizontal. On the surface of the horizontal plate knobs appear. A papilla (the dental papilla) is forming, by the growth of the connective tissue of the jaw, up into the thickened epithelium above it. It has been likened by Cunningham to an egg (the connective tissue) surmounted by an inverted egg-cup (the epithelial outgrowth or adamant organ). (*b*) The adamant organ, derived from the epithelium, continues to enlarge. Its derivation from the stratified epithelium is marked by a persisting bridge of epithelial cells (fig. 193, 9). Covering it, and continuous with this bridge, is

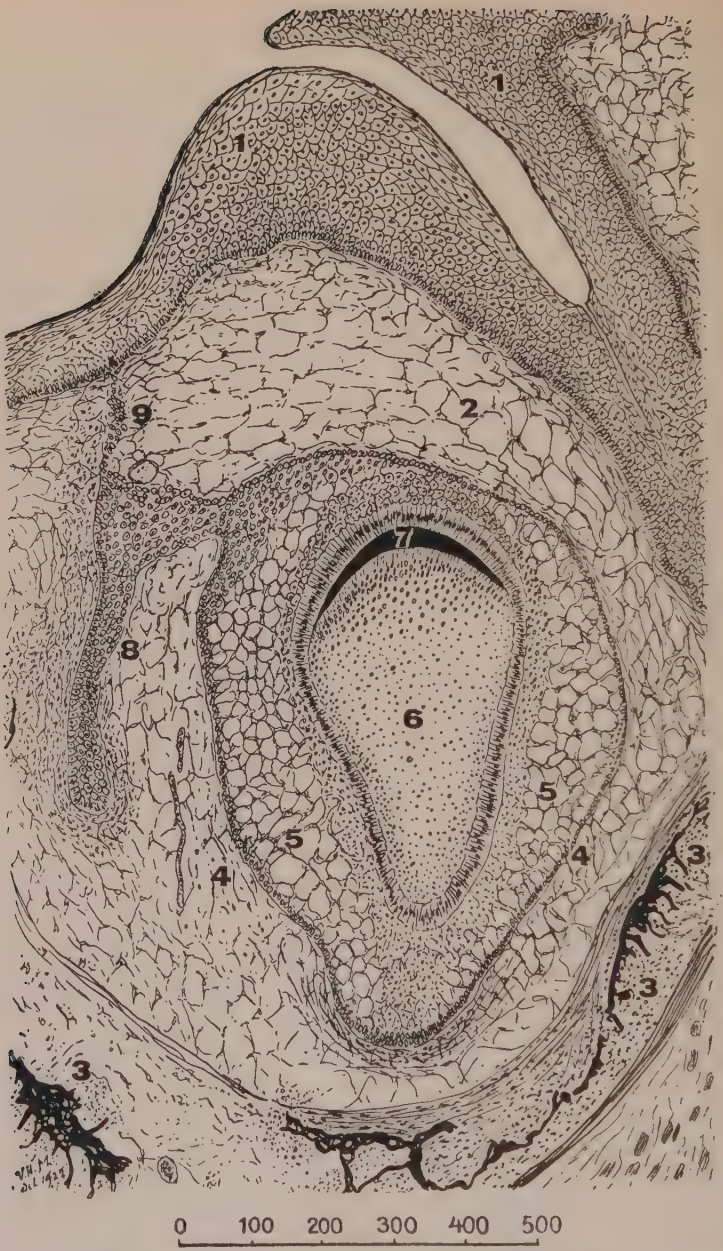



FIG. 193.—Developing milk tooth. $\frac{2}{3}'' \times 1$. W.M.C.

1, 1. Stratified epithelium of mouth. 2. Open mesh work of connective tissue. 3, 3, 3. Developing bone of jaw. 4, 4. Adamant or enamel organ, outer layer. 5, 5. Pulp of adamant or enamel organ. 6. Tooth pulp, containing masses of odontoblasts which manufacture the ivory or dentine of the tooth. 7. Layer of tissue externally consisting of adamant, laid down by the inner layer of the adamant organ, and internally of ivory, made by the odontoblasts of the pulp cavity. 8. Reserve germ for a permanent tooth. 9. Epithelial bridge between the dental germ and the parent epithelium.

formed a layer of epithelial cells. Within there is less differentiation. The cells form a reticulum, very much like a connective-tissue reticulum. This is termed the adamant or enamel pulp. Internally (and lining the inside of the egg-cup) the epithelium elongates into columnar cells, called adamant cells or ameloblasts. (*c*) Apposed against the ameloblasts is a layer of connective-tissue cells of the dental papilla. These, too, elongate into columnar cells. They begin to form ivory and are termed odontoblasts. Internally to these is the connective tissue of the dental papilla, or tooth pulp. Deposition of mineral matter at the surface between the ameloblasts and the odontoblasts begins. Externally, adamant is made, and internally ivory. This begins at the summit of the tooth and gradually extends downwards over the rest. As the layers of adamant and ivory increase the ameloblasts and odontoblasts retreat from each other. The adamant thus encroaches on the pulp of the adamant organ, and ivory on the dental pulp. The latter persists into adult life. Fibrillar branches of the odontoblasts remain within the ivory as the odontoblasts retreat. (*d*) The connective tissue around the tooth germ becomes more dense and vascular. It forms a bag around the developing tooth. Ossification of the jaw, too, goes on, and bone is formed around the teeth, so that the latter are in a bony groove, which later develops septa between the teeth. (*e*) When the crown of the tooth is completed the deposition of adamant ceases, but the deposition of ivory continues downwards to form the root. The substantia ossea (cement substance) is formed from the connective tissue of the dental sac, just as a periosteum forms a periosteal layer of bone in a developing bone. (*f*) Although the root is not completed, the tooth proceeds to erupt through the gum. Any bone which may have formed over the developing tooth—see (*d*) above—is absorbed and remodelled later on when the tooth assumes its final position. After eruption the formation of the root is completed. The permanent teeth are formed from an offshoot of the same invagination of epithelium, the reserve germ of which can usually be recognized from the first (see fig. 193).

## CHAPTER VII

# THE SENSORY APPARATUS

THE sensory apparatus of the body consists in general of two parts : (1) the sensory endings and the nerves to which they are attached ; and (2) a mechanism, simple or complex, consisting of epithelium, connective tissue or muscle cells, in which the nerve-endings are to be found. The function of this mechanism is to render the nerve fibres of that organ approachable by a special stimulus, and no other ; *to lower the threshold to the stimulus appropriate to that sense organ and to raise it to every other kind of stimulus* (Sherrington). Sometimes the sensory nerve ends around specialized cells in the end-organ (fig. 72), and sometimes epithelial cells of the end-organ are the sensory nerve cells and give rise to the sensory nerve (fig. 73). The variation in the mode of ending of the sensory nerves, both of shape and tissues in which they are found, has been briefly described (see p. 71). The simple blind endings there mentioned have no special mechanism for making them viable to specific stimuli. They are found in the epithelium of the cornea, and the tongue. In the skin they do not pass beyond the Malpighian layer. They occur, also, in serous membranes and in intermuscular septa. In all these examples the nerve fibre (medullated of course) divides dichotomously again and again as it reaches its destination, then loses its medullary sheath and eventually the neurolemma, and the fibrils of the axis cylinder, often varicose or moniliform, separate from each other and end blindly among or (perhaps) in the cells.

Sometimes the ending of the fibril is expanded into a plaque which fits on to specialized epithelial cells (tactile hairs and pig's snout), sometimes the endings are flowered or like ivy leaves, and sometimes, as around root-sheaths of hairs, a regular grid-iron-like plexus is formed. Simple specialized sensory apparatus is found in two types of " corpuscles,"

those of Meissner and Pacini. The former are found as oval bodies in the papillæ of the skin of the hand, forearm, foot, lips, and nipple, the conjunctiva of eyelids, and the mucous membrane of the tip of the tongue. Over the corpuscle (figs. 194 and 195) there is a connective-tissue sheath, which sends

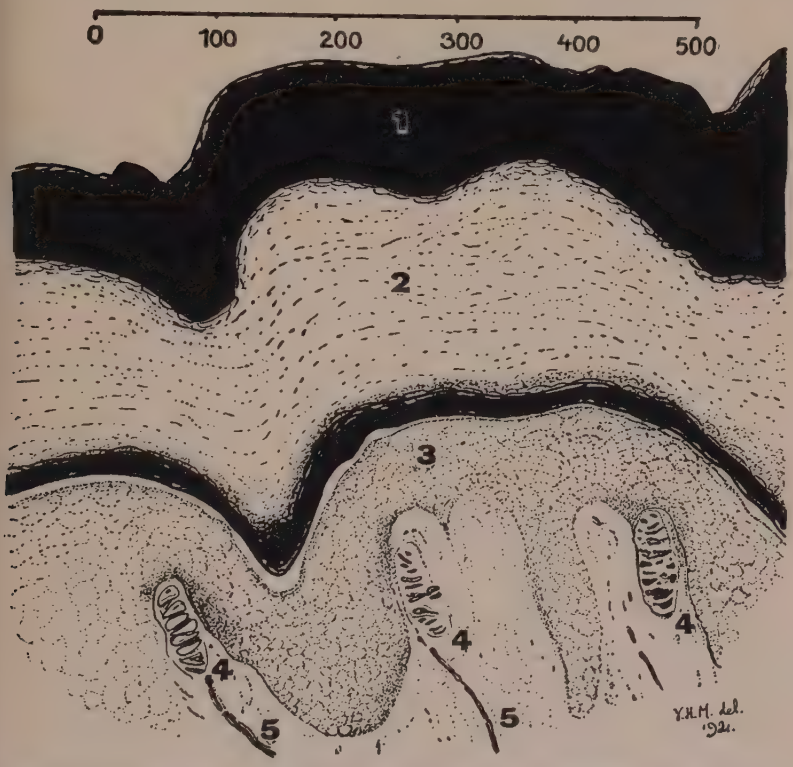



FIG. 194.—Meissner organs of touch in the skin (human). Osmic acid. $\frac{3}{8}'' \times 2$. C.

1. Outer layers of stratum corneum stained black with osmic acid. 2. Deeper layers of stratum corneum. 3. Rete mucosum of Malpighi. Between 2 and 3 are to be found the deepest layers of the stratum corneum and the stratum lucidum. 4, 4, 4. Meissner touch corpuscles. 5, 5. Medullated nerves running to the touch corpuscles.

down septa which incompletely divide the capsule into lobules. Within the capsule are to be found flattened wedge-shaped nucleated cells, piled one on the other, which look like epithelial cells.[1] One or two nerve fibres approach the

[1] Developmentally these cells derive from the mesoderm, and so no morphologist could admit them as epithelial cells.

corpuscle, penetrate through the capsule, lose their medullary sheaths, and then take a tortuous course through the core of the corpuscle. The axis cylinder divides and forms an inflorescence of expanded endings which lie between and around the epithelial cells of the core and near the surface of the corpuscle.

Fig. 195.—Meissner touch corpuscle. Osmic acid. $\frac{1}{8}''$ × 4. C.

1. Cells of the rete mucosum. 2. Sheath of corpuscle.
3. Wedge-shaped epithelial cell of corpuscle.
4. Connective tissue of the true skin—cutis vera.

More deeply, in the subcutaneous tissues of the body, we meet the tactile corpuscles of Pacini (fig. 196). They are found on the cutaneous nerves of the hand and the foot, the infraorbital and intercostal nerves, on the cutaneous nerves of the neck and mammary gland, and on the nerves of the solar plexus and of the joints. They are especially easy to observe with the naked eye in the mesentery of the cat. They are elliptical bodies, one or two millimetres long and two-thirds as broad. Each one is situate at the end of a medullated fibre. Under the microscope the corpuscle is seen to consist of concentric-lamellæ arranged around a clear central space. The lamellæ consist of fine connective tissue and are lined internally with nucleated pavement epithelium cells. Over the whole there is, too, a pavement epithelium. The central space is an elongated cylinder in shape, extending to near the distal end of the corpuscle. The

medullated nerve fibre passes axially through the corpuscle to the central space. The medullation ceases and the axis cylinder passes on towards the distal end of the central space. There it is terminated with a rounded knot or expansion, or it may branch and then be terminated by two knobs. Arteries have been described as penetrating the capsule.

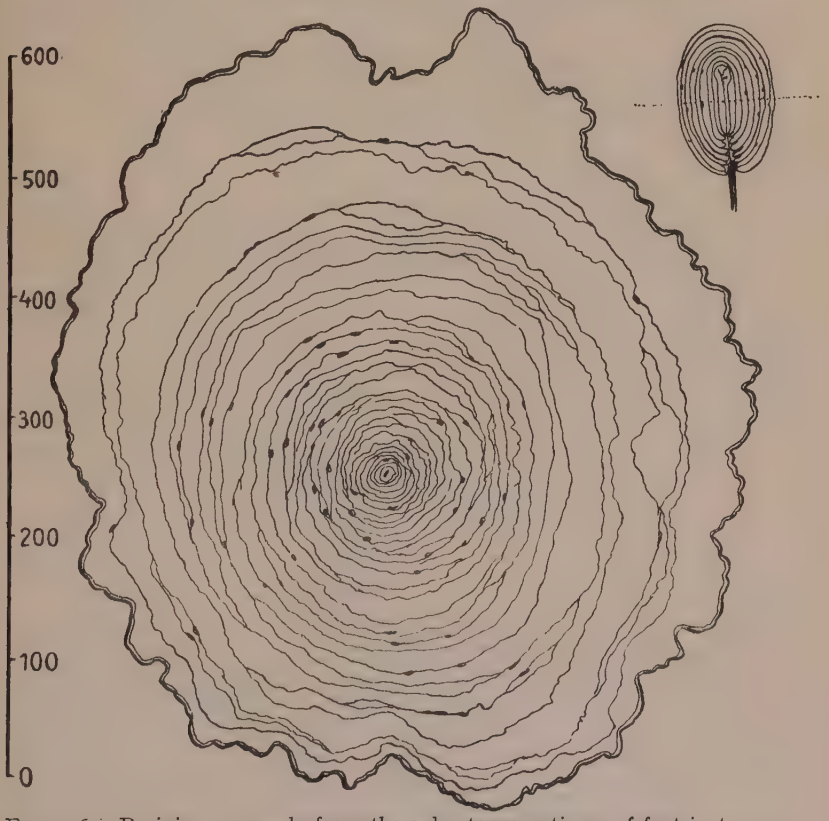



Fig. 196.—Pacinian corpuscle from the subcutaneous tissue of foot in transverse section. Osmic acid. $\frac{2}{3}'' \times 4$. C.

The corpuscle consists of concentric layers around a central core, into which the nerve passes. The osmic acid used in fixation has caused considerable crinkling. At the upper right-hand corner is a diagram of a Pacinian corpuscle magnified about twelve times and seen in longitudinal section. The dotted cross line represents the plane in which the corpuscle drawn under the $\frac{1}{3}''$ objective was seen.

**Muscle Sense**—Sensory apparatus, specialized for registering the contraction of skeletal muscles and the disposition of the joints of the body, is found in muscle and on the tendons. Fig.

197 shows the muscle-sense organ, known as a muscle spindle. These are found buried in skeletal muscle as long fusiform bodies running parallel with the general direction of the muscle fibres. (For their position and appearance in cross section,

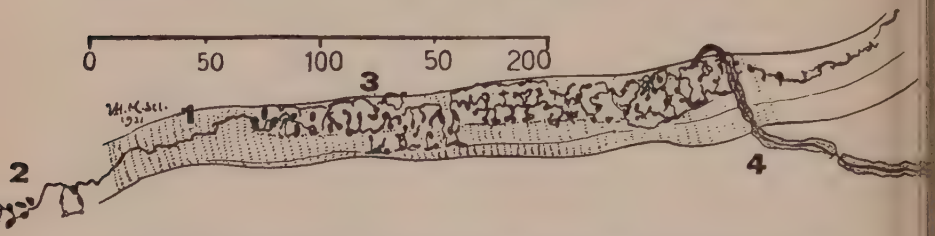



FIG. 197.—Muscle spindle in teased preparation made with gold chloride. $\frac{1}{6}''$ × 1. C. (See also fig. 52 for muscle spindle in transverse section.)

1. Fibres of cross-striated muscle, rather smaller than the normal. 2. Flowered nerve endings. 3. Nerve-endings of the annulo-spiral type. 4. Medullated sensory nerve.

see fig. 52.) They are covered with a sheath of connective tissue, which carries in addition nerve fibres and blood vessels. Internally there are two or three long, narrow, cross-striated muscle fibres, sometimes branched at one end. Their diameter

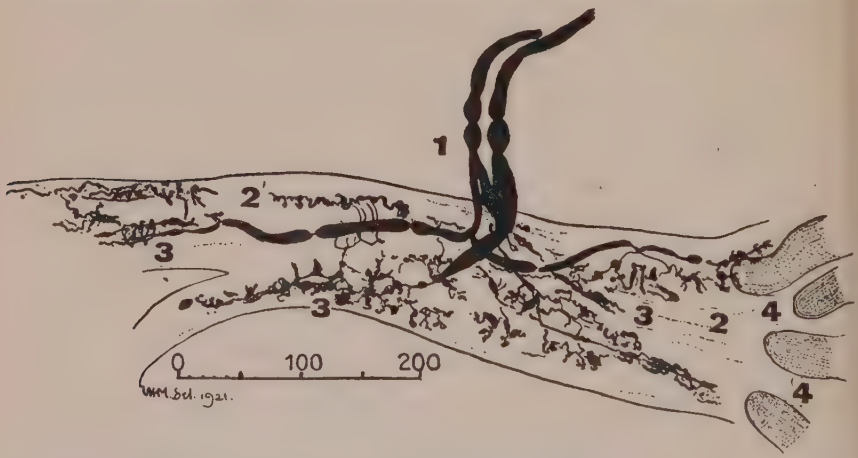



FIG. 198.—Golgi tendon organ. Gold chloride. $\frac{2}{3}''$ × 4. C.

1. Two medullated nerve fibres running from tendon. 2, 2. Tendon. 3, 3, 3. Nerve endings of the tendon. 4, 4. Muscle fibres inserted into the tendon.

is not more than a half of that of the ordinary muscle fibres, and often less. Further, the nuclei of these fibres are sometimes within the substance of the fibre and not peripheral. In other

words, the muscle fibres within the spindle are of an embryonic type. Sensory fibres pierce the connective-tissue sheath and end on the surface of these muscle fibres.

When the muscle is stained with gold chloride and teased, we get an appearance as shown in fig. 197. There are seen in that figure two striped muscle fibres and a medullated fibre passing to one of them. It loses its medullation. The axis cylinder passes for a few $\mu$ unbranched, and then branches into a most complex tangle of endings. They can be resolved

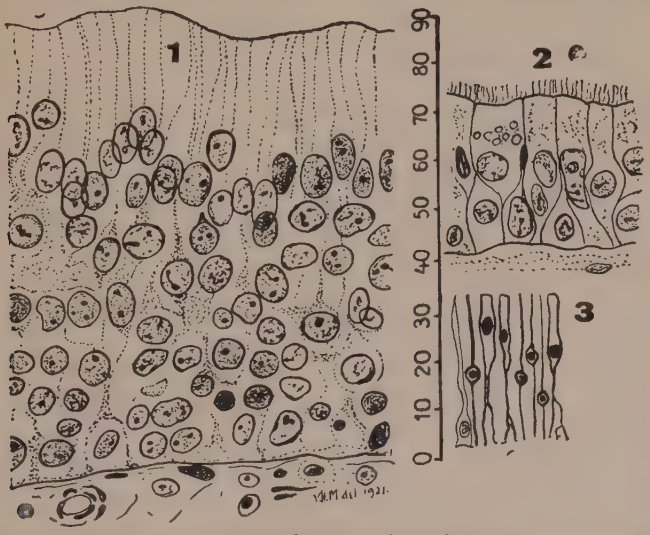



FIG. 199.—Olfactory mucous membrane and respiratory mucous membrane. $\frac{1}{8}'' \times 4$. C.

1. Olfactory mucous membrane. 2. Adjacent respiratory mucous membrane drawn to the same scale. 3. Small-scale interpretation of olfactory mucous membrane.

into two types: (1) the annulo-spiral endings, which grip the muscle fibre; and (2) the flowered endings, which are formed at some distance from the main mass and lie on the surface of the fibre. The first set is almost certainly stimulated by change in the cross section of the fibre it supplies, and the second, perhaps, by change in length.

Similar apparatus is seen in the Golgi tendon organ (fig. 198). Close to the junction of muscle and tendon sensory fibres are distributed to the tendon. These branch once or twice, retaining the medullation. Then the medullation ceases, but each axis cylinder passes on, branches di- or tri-chotomously

and then forms complex varicose endings, often running a considerable distance along the general direction of the tendon fibrils.

A much simpler type of ending is found in the **olfactory** mucous membrane. The olfactory region of the nasal mucous membrane is that covering the upper third of the septum and the surfaces of the superior and middle turbinate bones. There is an abrupt passage from epithelium of the respiratory type to that of the olfactory type (which is much taller), and the mucous membrane is pigmented with a yellow pigment. Fig. 199 shows the two types of epithelia contrasted. The olfactory epithelium is approximately 100$\mu$ deep, whereas the

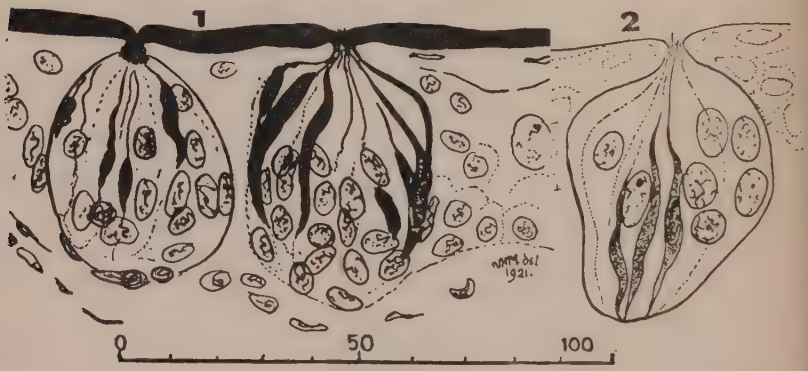



FIG. 200.—Taste-buds. $\frac{1}{8}$" × 4. C.

1. Two adjacent taste-buds, stained with iron-hæmatoxylin. 2. Similar taste-bud from another preparation fixed in osmic acid and not stained.

respiratory is little more than 30$\mu$. When teased the olfactory epithelium is found to be but one cell deep, the numerous nuclei being due to the arrangement of the nuclei of the different columnar cells at different levels. The cells are of two types: (1) columnar cells standing upon the basement membrane and supporting the second type; (2) bipolar cells whose upper end projects a little beyond the surface of the epithelium, and whose lower end is continued onward into the olfactory nerve (see fig. 73). These cells are epithelial cells specialized for sensory function, and not only originating but conducting a nervous impulse. Such was probably an early type of differentiation of function.

The **gustatory** organs are distributed over the tongue and occur, too, though more rarely, on the soft palate. They are

FIG. 201.—Portion of the anterior part of the eye. $\frac{3}{8}$" × 1. K.C.W.

1. Part of eyelid. 2, 2. Cornea. 3. Canal of Schlemm. 4. Ligamentum pectinatum. 5. Ciliary muscles, etc. 6, 6. Ciliary processes. 7. Suspensory ligament which has torn away from the lens. 8. Iris. 9. Lens. 10. Sphincter muscle of the iris. [Note the different types of epithelium on the eyelid, the sclerotic, the cornea (anterior and posterior surfaces), and on the lens.]

(For surface view of the corneal corpuscles, see fig. 36.)

curious, flask-shaped groups of cells (fig. 200), in the stratified edithelium called taste-buds, and extending from its inner to its outer surface. They are generally found in the furrows around the fungiform and circumvallate papillæ. They contain two types of cells: (1) long, flattened, tapering cells, extending from the base of the taste-bud to the orifice, with spherical nuclei; and (2) spindle-shaped "gustatory" cells, with oval nuclei, having the upper filamentous end projecting from the orifice of the taste-bud. Unlike their analogues in the olfactory mucous membrane, their lower extremity is not continuous with the fibres of the gustatory nerve fibres. The latter penetrate into the taste-bud and the branchings of their naked-axis cylinders end around the gustatory cells.

When we turn to the eye and ear, we find that the apparatus surrounding and protecting the sensory end organs from inappropriate stimuli and directing appropriate stimuli upon them is much more complicated. To deal with them is more the function of macroscopic than of microscopic anatomy. But some of the structures involved are of interest and importance to the histologist. Those in the eye are the anterior portion and the retina, and in the ear the organ of Corti.

The outer coat of the **eye,** the sclera or sclerotic, consists of bundles of white fibrous tissue, closely interlaced at right-angles to each other. In front it is continued into the cornea, and at the junction is found a circular canal lined with endothelium, known as the sinus venosus scleræ, or canal of Schlemm (fig. 201, 3). In the angle between cornea and iris will be found spaces which communicate on the one hand with the anterior chamber of the eye, and on the other with this canal, forming the means by which the aqueous humour of the anterior chamber finds its outlet into the veins. The cornea is a transparent tissue composed of five layers. Externally there is a stratified epithelium consisting of six to eight cells continuous with that of the sclera and the conjunctiva, but not so thick (see fig. 201). Immediately interior to this is an elastic layer. Then follows the substantia propria or chief substance of the cornea. This consists of a highly modified connective tissue arranged in lamellæ, with a homogeneous interstitial substance binding the fibres together. Between the lamellæ, and spindle-shaped in cross section,

are the flattened connective-tissue corpuscles of the cornea. These are stellate cells with long processes communicating with those of their neighbours (see fig. 36). Next in order comes the posterior elastic lamina, which, at the sclero-corneal junction, splits into bundles of interlacing fibres known as the ligamentum pectinatum (fig. 201, 4), in the meshes of which are the spaces of the angle of the iris already noted. Finally, the cornea is covered internally with an endothelium of flattened polygonal cells, continuous with that covering the iris and lining the spaces of the angle of the iris.

The second coat of the eye is the choroid coat, consisting of three layers. From without inwards these are : (1) a layer of elastic fibres with pigment cells in the meshes ; (2) the main layer of the choroid, consisting externally of blood vessels, numerous pigmented cells, connective tissue, elastic fibres, and some unstriped muscle, and internally of a capillary network ; and (3) the basal lamina, transparent, thin, and nearly structureless. Towards the region of the corneo-sclerotic junction the choroid coat thickens and is continued into the ciliary body. This connects the choroid to the circumference of the iris (see fig. 201). The ciliary body consists of the orbiculus ciliaris, the ciliary muscle, and the ciliary processes. The ciliary muscle consists of radial (meridional) and circular fibres, both of which by contraction relax the suspensory ligament. The ciliary processes are projections of the ciliary body. They contain numerous tortuous capillaries and are deeply pigmented. The pigment is confined to a layer of columnar epithelium, pars ciliaris retinæ, two cells deep, continuous with the third coat of the eye, the retina. The epithelium is invaginated to form glands which presumably secrete the aqueous humour.

The ciliary processes are closely apposed to the surface of the vitreous humour so that its membrane, which forms the suspensory ligament of the lens, often tears away with that part of the eye in process of preparation (see 6, fig. 201).

The ciliary body is connected directly with the iris, a circular contractile diaphragm, pierced with a circular aperture, the pupil. On its anterior surface is an endothelium continuous with that of the cornea. The posterior surface is covered with two layers of columnar pigmented epithelium, continuous with that of the ciliary processes. The main body of the iris consists of delicate connective tissue and elastic fibres, with

very numerous pigment cells, blood vessels and nerves. There are two sets of muscle fibres (unstriped) in the iris : (1) radial, (2) circular. The radial are difficult to observe. They extend inwards from the ciliary margin of the iris towards the pupil. The circular fibres are seen as a compact mass (10, fig. 201) near the aperture of the pupil.

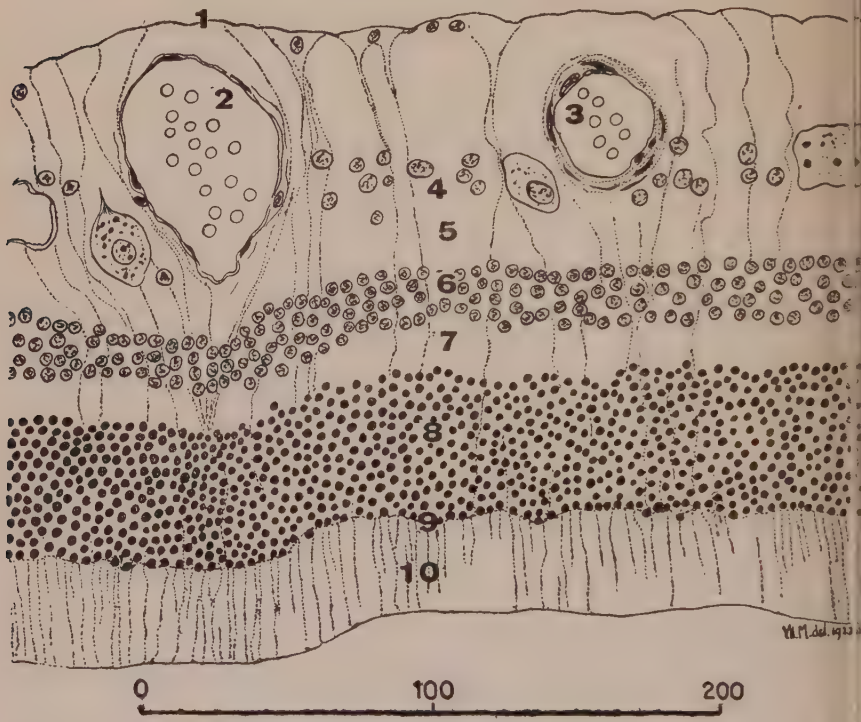



FIG. 202.—Retina. $\frac{1}{8}$" × 2. K.C.W.

1. Internal limiting membrane, beneath which is a layer of nerve fibres. 2. Vein with red blood corpuscles. 3. Artery. 4. Ganglion cell layer. 5. Inner molecular layer. 6. Inner nuclear layer. 7. Outer molecular layer. 8. Outer nuclear layer. 9. External limiting membrane. 10. Layer of rods and cones.

[Note.—In forming an image on the retina the rays of light pass from above towards 10.]

The third coat of the eye, the retina, is a thin, delicate membrane, spread out on the inner surface of the eye, and contains the nervous elements responsible for vision. At the blind spot it is pierced by the optic nerve and concomitant blood vessels. These, blood vessels and nerves, spread themselves fan-wise out over the inner surface of the retina.

Towards the front of the eye the retina appears to end in the ora serrata. Here the nervous elements end, but the retina is carried on over the ciliary body to the iris. The retina, in its posterior portion, consists of ten layers (fig. 202):

(1) (From within—i.e. near the vitreous humour and towards the lens) the internal limiting membrane, consisting of the expansion of the ends of supporting cells which pass from back to front of the retina and keep its elements in position.

(2) A layer of nerve fibres deriving from the optic nerve. In this layer are found the blood vessels (figs. 202, 2 and 3) supplying the retina.

(3) The ganglionic layer, consisting of rather large nerve cells, the axis cylinders of which pass into and form the optic nerve (fig. 202, 4).

(4) The inner molecular layer, or layer of dendrons and synapses of the cells of the third and fifth layers (fig. 202, 5).

(5) The inner nuclear or granular layer, consisting of the cell bodies and nuclei of small bipolar cells, whose processes extend from the fourth to the sixth layer only (fig. 202, 6).

(6) The outer molecular layer, which, like the fourth layer, consists of dendrons and synapses.

(7) The outer nuclear or granular layer, consisting of the nuclei of the sensory end apparatus, the rods and cones.

(8) The external limiting membrane, the expansion of the far ends of the supporting cells mentioned in layer 1.

(9) The layer of rods and cones (fig. 202, 10).

(10) The pigment cell layer, consisting of cells fixed to the inner layer of the choroid coat, with spherical nuclei and a clear protoplasm surrounding the nuclei, but, distally, highly pigmented processes, which pass down between and around the rods and cones (fig. 203, 9).

The structure of the rods and cones is not usually demonstrable in the ordinary preparation of the retina. The elements must be teased out and require special staining. They are sometimes more visible in the retina of the dark-adapted eye (see fig. 203). In such a retina most of the rods and cones move up into the pigment of the pigment cells, but not all. On staining with picrocarmine, those left behind are visible. In the preparation from which fig. 203 was made, the cones were demonstrable. They are seen to consist of a barrel-shaped inner segment, surmounted with a cone like a dunce's cap. This gives the element its name. The rods also consist of

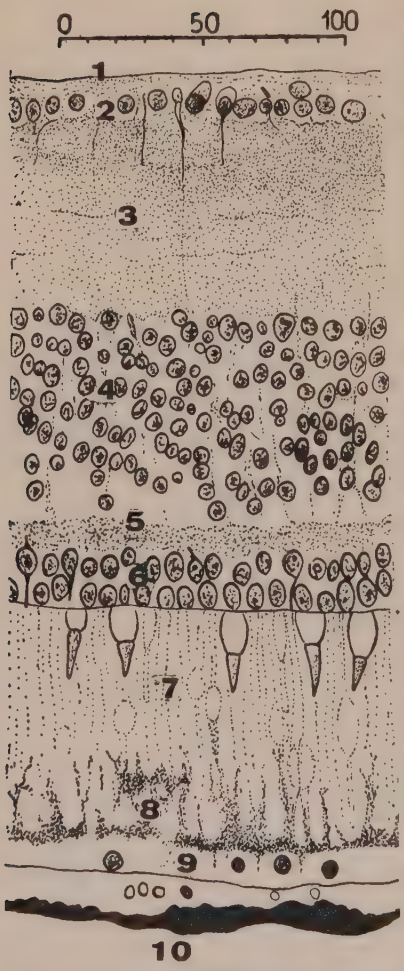



FIG. 203.—Frog's retina fixed in the state of dark adaptation. $\frac{1}{6}$″ × 2. C.

1. Internal limiting membrane. 2. Layer of ganglion cells. 3. Inner molecular layer. 4. Inner nuclear layer. 5. Outer molecular layer. 6. Outer nuclear layer. 7. Layer of rods and cones. 8. Pigment. 9. Pigment epithelium. 10. Choroid coat.

Five cones are seen which have remained in proximity to the external limiting membrane, the others and the rods have extended towards and into the pigment of the pigment-producing epithelium.

an inner and an outer segment. The inner is much more slender than that of the cone, and the outer segment is much taller and more slender. The nuclei of the rods and cones are found in the outer nuclear layer, that of the cone being situate immediately beneath the inner segment and outer limiting membrane. That of the rod is some distance away (see diagram, fig. 73).

The end apparatus of the acoustic nerve is of two types, according to the functions performed by the nerve fibres. If their function is **proprioceptive,** i.e. either to keep the sensorium aware of the head's static position or of its movements in space, the sensory endings are similar in plan to those of the gustatory nerves. The axis cylinders of fibres end, after considerable branching, among highly specialized epithelial cells. In the ampullæ of the semicircular canals, there are patches where the epithelium, which is normally somewhat flattened, consists of tall epithelial cells (compare the olfactory epithelium), supported by sustentacular cells, and surmounted by a tapering mass of hairs projecting into the

endolymph of the membranous labyrinth. Around these cells the endings of the vestibular part of the acoustic nerve are found.

In the saccule and utricle the epithelium is similar, but in addition there is over it a mucus-like cap, containing tiny crystals of calcium carbonate, known as otoliths.

If the function of the fibres is **auditory,** they end in the cochlea in the curious organ of Corti, which merits close

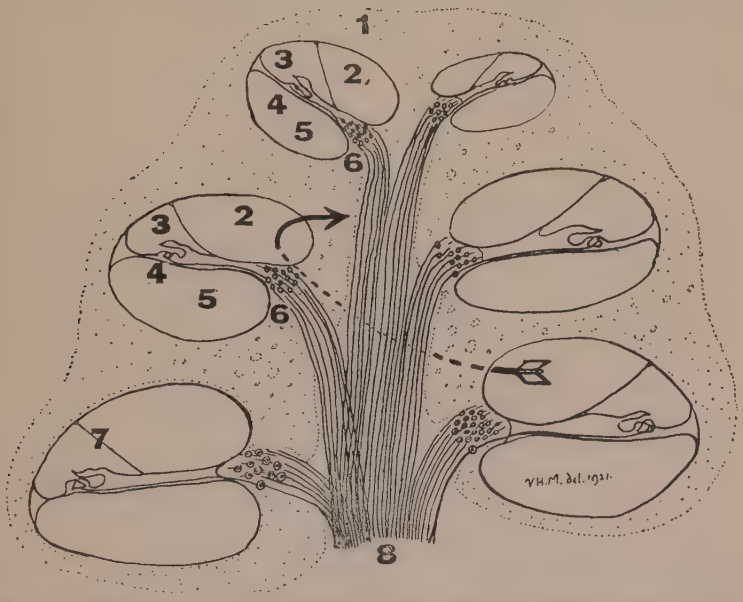



FIG. 204.—Diagram of the cochlea to show the arrangement of the whorls, position of the organ of Corti, and of the ganglion cells and nerve fibres.

1. Bone. 2, 2. Scala vestibuli. 3, 3. Canal or duct of the cochlea. 4, 4. Organ of Corti. 5, 5. Scala tympani. 6, 6. Spiral ganglion. 7. Reissner's membrane. 8. Cochlear nerve.

attention. The position of this organ is shown in fig. 204. It is situate in a spiral canal of triangular cross section (3, fig. 204), cut off from the perilymph above by a delicate membrane (membrane of Reissner or membrana vestibularis), and below by a thicker membrane, the basilar membrane. Looking at the organ (organon spirale or organ of Corti) more closely, we see (fig. 205) that the epithelium is much thickened at this point. Through this epithelium there is a spiral tunnel of triangular cross-section formed by two sets

of ossicles (6 and 9, fig. 205), each pair of which is arranged as a Gothic arch. Immediately under this is the basilar membrane, containing a vein (vas spirale). In the thickened

FIG. 205.—Organ of Corti. $\frac{1}{8}$" × 2. C.

1. Scala vestibuli (cp. fig. 204). 2. Reissner's membrane, somewhat collapsed. 3. Membrana tectoria. 4. Spiral sulcus. 5. Inner hair cell. 6. Inner rod. 7. Basilar membrane. 8. Blood vessel. 9. Outer rod. 10. Outer hair cells. 11. Stria vascularis. 12. Scala tympani.

epithelium on each side of the tunnel are hair cells; one on the inner side supported by elongated epithelial cells, and four on the outer side. The supporting cells—sustentacular

cells—together with the expansions of the heads of the rods of Corti, form a membrane, the reticular membrane, through apertures in which the hairs of the hair cells project. Around the lower end of these hair cells, the outer processes of bipolar cells, situate in the spiral ganglion, end. They reach the hair cells by passing along the spiral lamina and the inner portion of the basilar membrane and transversely through the tunnel. Over the spiral organ is a membrane called the membrana tectoria. It reaches, in a perfect preparation, as far as the outer hair cells—in fig. 205 its tip has curled backwards—and according to Retzius is attached to the sustentacular cells which alternate with the outer row of hair cells.

In the human cochlea the width of the basilar membrane increases from 210$\mu$ in the lower whorls of the cochlea to 360$\mu$ in the upper, and there are in it 24,000 distinct fibres. There are 6000 inner rods and 4000 outer rods, 3500 inner hair cells, and 12,000 outer hair cells. These figures are given because of their bearing on theories of hearing. There is no doubt that there is in the ear, probably in the cochlea, a resonating mechanism. There must be one resonating element for each distinguishable note, and the basilar fibres are the only elements of which there are sufficient numbers.

## CHAPTER VIII

# THE CENTRAL NERVOUS SYSTEM

OF the whole range of tissues to be studied histologically, that of the central nervous system is the most complicated at first sight. Fundamentally, the elements of which it is composed are simple. They are nerve cell bodies (perikarya) and their projection fibres (dendrons and axons), with a specialized type of connective tissue, neuroglia. Externally there is ordinary connective tissue, and blood vessels penetrate into the substance of the central nervous system. But it is the protean shapes of the nerve cells and the extents of their projection fibres, the groupings of nerve cells into ganglia and "nuclei," the complication of cross connexions between the ganglia and nuclei [1] that produce such bewilderment in the mind of the student beginning the study of the central nervous systems.

There are two ways of learning the histology of the central nervous system. Either one may take a number of sections of it at different levels and memorize the names, often apparently arbitrary, of the different structures seen; or one may attempt to group the facts on some definite plan or hypothesis. In the long run the latter method is the one that works, and is the one that will be indicated and followed in the text. It is simplest to treat the central nervous system from its developmental and functional aspects.

On the whole, the arrangement of the body is based on wonderful common sense. But we have to remember that the history of the body from immemorial time has played great part in determining the arrangement of organs. The laws of structure and function have broadened down from precedent to precedent. The body frequently has had to adapt organs already there to a newly arising need and purpose, rather than

[1] The term "nucleus" in the central nervous system terminology means a definitely recognizable group of nerve-cells and is thus practically equivalent to the term "ganglion," which is retained, mainly, for groups of nerve cells outside the central nervous system. See pp. 73 and 74.

to invent *de novo* a new apparatus. Doubtless, if we had to invent a nervous system it would appear more symmetrical and reasonable than the present one. Such a complexity as the use of three different nerves—the oculo-motor, the trochlear, and the abducens—to activate the muscles of the eye, would be avoided. But for such complexities there is embryological ground, and the student should consult a textbook of anatomy (e.g. Cunningham's) for a simple dia-

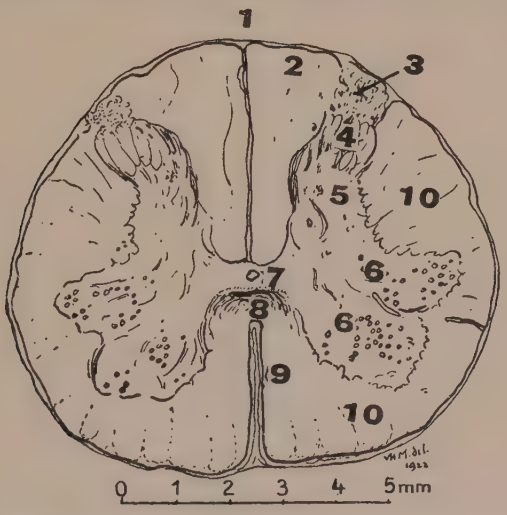



FIG. 206.—Transverse section of the spinal cord in the lumbar enlargement. × 7. G.A.H.

(Numerical order.) [1]

1. Posterior median sulcus and septum. 2. Fasciculus gracilis (Goll's column). 3. Posterior root nerve fibres. 4. Substantia gelatinosa of Rolando. 5. Posterior column (of grey matter) or posterior horn. 6, 6. Anterior column or horn, showing numerous groups of motor nerve cells. 7. Central canal and grey commissure. 8. Anterior (white) commissure. 9. Anterior median fissure. 10. Fasciculi of white fibres.

(Alphabetical order.)

Anterior column or horn, 6, 6. Anterior median fissure, 9. Anterior (white) commissure, 8. Central canal, 7. Gracilis, fasciculus, 2. Grey commissure, 7. Goll's column, 2. Motor nerve cells, 6, 6. Posterior column or horn, 5. Posterior median sulcus and septum, 1. Posterior root nerve fibres, 3. Substantia gelatinosa of Rolando, 4. White fibres, fasciculi of, 10.

grammatic account of the origin of the sensory and motor nerves, and their position and roots in the nervous system, and especially of the modification of the plan found among the cranial nerves. The latter should banish the trouble of remembering in exactly what position the nuclei of the various cranial nerves are to be found.

[1] In this, and following diagrams, as indeed in most diagrams of this book, an attempt has been made to keep No. 1 near the top of diagram and to work in a clockwise spiral, or similar direction, away from it.

Then the functions of the whole and the various parts of the central nervous system will aid in remembering the anatomical connexions between them. For instance: broadly the function of the central nervous system is to originate a response to a change in the environment. For this you must have *conduction* of a sensory nervous impulse to the nerve cells which will originate an appropriate response. And further, as a response by one set of muscles may necessitate alteration of the state of antagonistic muscles of the same side, or of

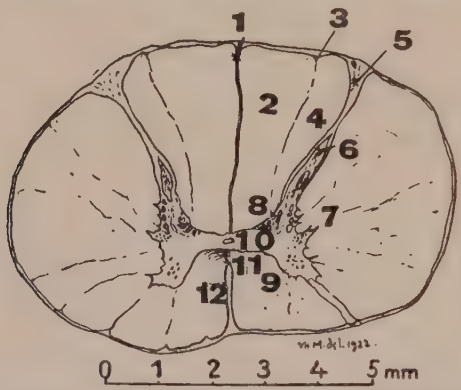



FIG. 207.—Transverse section of the spinal cord in the mid-thoracic region. × 7. G.A.H.

(Numerical order.)

1. Posterior median sulcus and septum. 2. Fasciculus gracilis (Goll's column). 3. Postero-intermediate sulcus and septum. 4. Fasciculus cuneatus (Burdach's column). 5. Postero-lateral sulcus and posterior nerve root. 6. Substantia gelatinosa of Rolando. 7. Lateral column (or horn). 8. Dorsal nucleus (Clarke's column). 9. Anterior column. 10. Central canal and grey commissure. 11. Anterior (white) commissure. 12. Anterior median fissure.

(Alphabetical order.)

Anterior column, 9. Anterior median fissure, 12. Anterior (white) commissure, 11. Burdach's column, 4. Central canal and grey commissure, 10. Clarke's column (dorsal nucleus), 8. Cuneatus, fasciculus, 4. Dorsal nucleus (Clarke's column), 8. Goll's column, 2. Gracilis, fasciculus, 2. Grey commissure and central canal, 10. Lateral column (or horn), 7. Nerve root, posterior, and postero-lateral sulcus, 5. Posterior median sulcus and septum, 1. Postero-intermediate sulcus and septum, 3. Postero-lateral sulcus, 5. Substantia gelatinosa of Rolando, 6.

symmetrical muscles of the opposite side, or of the trunk, or of other limbs, and neck, head, and eyes, the original sensory impulse must be able to affect the motor nerve cells of all these groups of muscles. So there must be commissures and tracts within the nervous system *co-ordinating* the activities of the various parts. Such considerations aid us in disentangling the complexities of the central nervous system.

As an example, take the three sections of the spinal cord (figs. 206, 207, 208). They are from the lumbar swelling, mid-thoracic region, and cervical swelling of the spinal cord.

Why the difference in appearance? They will be seen to consist of an inner butterfly-shaped figure set in an oval. The butterfly consists of *grey matter*, i.e. of nerve cells, their dendrons and synapses and neuroglia. The function of nerve

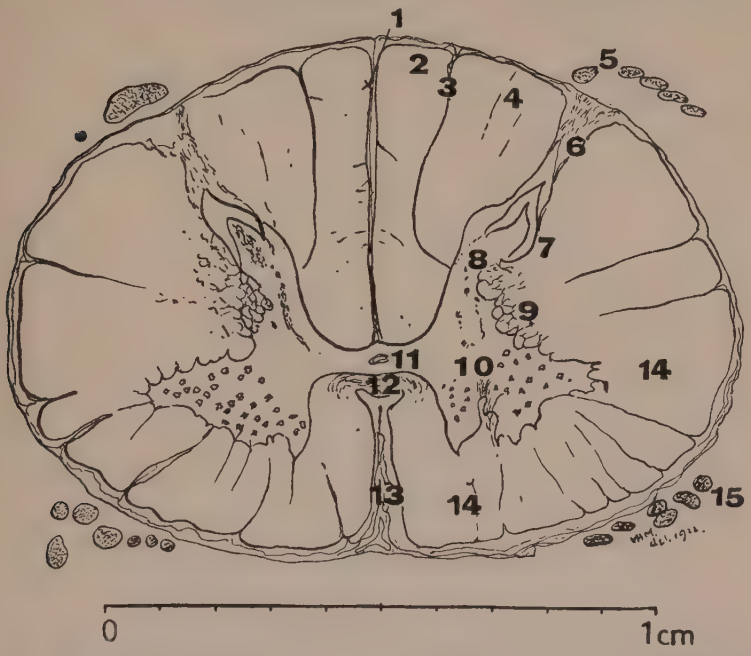



FIG. 208.—Transverse section of the spinal cord in the cervical enlargement. × 7·2. G.A.H.

(Numerical order.)

1. Posterior median sulcus and septum. 2. Fasciculus gracilis (Goll's column). 3. Postero-intermediate sulcus and septum. 4. Fasciculus cuneatus (Burdach's column). 5. Posterior nerve-root fibres. 6. Posterior nerve-root fibres entering cord. 7. Substantia gelatinosa of Rolando. 8. Posterior column or horn. 9. Formatio reticularis. 10. Anterior column (or horn) with numerous groups of motor nerve cells. 11. Central canal and grey commissure. 12. Anterior (white) commissure. 13. Anterior median fissure. 14, 14. Fasciculi of white fibres. 15. Anterior root fibres.

(Alphabetical order.)

Anterior column (or horn) with motor nerve cells, 10. Anterior median fissure, 13. Anterior (white) commissure, 12. Anterior root fibres, 15. Burdach's column, 4. Central canal and grey commissure, 11. Cuneatus, fasciculus, 4. Formatio reticularis, 9. Goll's column or fasciculus gracilis, 2. Motor nerve cells, 10. Posterior column or horn, 8. Posterior median sulcus and septum, 1. Posterior nerve-root fibres, 5. Posterior nerve-root fibres entering cord, 6. Postero-intermediate sulcus, 3. Substantia gelatinosa of Rolando, 7. White fibres, fasciculi of, 14, 14.

cells is that of keeping the cell processes alive so that they may originate nervous impulses. The function of the dendrons is correlation and co-ordination.[1] The oval area outside the

[1] For explanation of terminology see p. 64.

grey matter is *white matter*, or nerve cell axones, whose function is conduction. The lumbar and cervical swellings are the positions in the spinal cord at which the nerves from and to the lower and upper limbs respectively enter or leave the spinal cord. Consequently we should expect more grey matter at the swellings than elsewhere in the cord. It is patent from the figures that this is so. Both the posterior column of grey matter (sensory) and the anterior column are much enlarged (cp. figs. 206, 6, and 208, 10, with fig. 207). Further, all the grey matter with the large nerve cells in it in the anterior columns in the two swellings is *additional* to that seen in fig. 207. It is reasonable to suppose that these nerve cells activate the muscles of the respective limbs. Experiment shows that this is so.

The next point that arises is: in what way do the cervical and lumbar swellings differ? In managing the body the ganglia at the upper (forward) end of the nervous system have gained control over the activities of the body. The brain dominates the spinal cord, and not vice versa. Consequently all sensory fibres which enter the spinal cord must connect upwards towards the brain, in addition to making contact at their level of entrance. Therefore at the cervical level there will be more fibres conducting impulses upwards than at the lumbar level, for there will be, in addition to those entering at the lumbar level, all those entering in the thoracic and at the cervical level. Similarly with the fibres for conducting motor impulses. They come down from the cerebral hemispheres. Those activating muscles in the arm end in the cervical region, those activating the trunk leave in the thoracic region, and those activating the legs leave in the lumbar region. Consequently at the cervical region there are more fibres for conducting motor impulses than at the lumbar swelling. So on both counts there are many more conducting elements at the cervical level than at the lumbar level; i.e. there must be *more white matter*. It is clear from figs. 206 and 208 that this is so; there is at least two and a half times as much white matter.

The point has been somewhat laboured, and although many other illuminating instances could be given of the mnemonic use of physiology in the study of the histology of the central nervous system, the above must suffice. But the student is counselled to have at hand good textbooks of

embryology or anatomy and physiology, when reading the complex histology of the central nervous system.

Turning to fig. 206 (a cross section of the spinal cord in the lumbar region), we note that the whole is covered with a connective-tissue sheath: the pia mater. This sends septa down into the substance of the cord, the most complete being the posterior median septum which passes down in the median line as far as the grey matter. On the anterior side there is the anterior median fissure, passing almost, but not quite, to the grey matter. The pia mater is vascular and the blood vessels accompany the septa that it sends down into the white matter. Approximately in the centre of the section is the central canal continuous with the ventricles of the brain. This is lined with ciliate epithelium—the ependyma. The central canal is placed in a mass of grey matter forming a bridge (fig. 206, 7), between the masses of grey matter in each half of the spinal cord. This bridge is known as the grey commissure. It consists mainly of neuroglia, but commissural fibres can be seen to connect the grey matter on the two sides (e.g. collaterals—dendrons—of sensory nerve fibres pass across here to connect with motor cells of the opposite side, in order to activate muscles on the opposite side of the body: see above). Joined by this commissure are two roughly crescentic masses of grey matter. The anterior portion of the crescent (anterior column of grey matter or anterior horn) is much blunter than the posterior column. In the anterior column are to be seen large stellate nerve cells arranged in groups, and, frequently, axons may be seen passing out radially into the white matter. The nerve cells are motor in function and the axons are the motor nerve roots ("anterior" roots) passing out on their way to the muscles of the lower limbs, etc. The posterior column is surmounted with a cap of deeply staining material, the substantia gelatinosa of Rolando. This forms a useful landmark where it appears. It consists of neuroglia with very numerous small nerve cells, around which collaterals of the entrant ascending and descending sensory fibres (3, fig. 206) end. In the posterior horn will be found larger stellate cells, also in communication with sensory nerve collaterals, and from these spring axons which travel up the cord, mainly on the opposite side.

The white matter consists of medullated nerves, mainly of large calibre. There is no neurilemmar sheath. The nerve

fibres pass, longitudinally for the most part, up and down the cord, the exceptions being (1) where the sensory nerve fibres are entering the cord; (2) where the motor fibres leave the anterior horn; and (3) where they pass from one side of the cord to the other, around the end of the anterior median fissure. This crossing is called the anterior white commissure (8, fig. 206), but is really a decussation (see later).

Passing to the thoracic region we see that (1) the cord is smaller in cross section; (2) it is oval; (3) the central canal is nearer the anterior surface; and (4) the grey matter is much more slender. Otherwise the plan is the same. In the grey matter there is a new group of cells close to the root of the posterior column on the medial side. This is known as the dorsal nucleus or Clarke's column. It should be called the *thoracic* nucleus. It consists of torpedo-shaped cells placed vertically, and gives rise to an important tract of fibres in the lateral part of the spinal cord, known as the spinocerebellar fasciculus or direct cerebellar tract of Flechsig. There is further a column of cells forming a projection (the lateral horn) between the posterior and anterior columns. This, too, is characteristic of the thoracic part of the spinal cord. The column is termed, from its position, "intermedio-lateral." The cells in it give rise to small medullated fibres, which pass out into the anterior root and are viscero-motor (sympathetic) in function. The groups of large cells are naturally absent from the anterior column.

The white matter is greater in amount, and in the posterior region shows a definite separation into two columns, the postero-median or fasciculus gracilis (Goll's column) and the postero-lateral or fasciculus cuneatus (or Burdach's column). In the region above the lateral column there is some fraying out of the grey matter into the white (more conspicuous higher up), which is termed the formatio reticularis (or reticular formation).

The cervical swelling is in some respects similar to the lumbar swelling, but: (1) the cord is elliptical; (2) the central canal is one-third of the way along the short diameter from the anterior side; (3) the grey matter is more clean-cut and the substantia gelatinosa is cone- and not cabbage-shaped; (4) the formatio reticularis is well marked; (5) there is much more white matter in relation to the grey; and (6) the gracile

and cuneate fasciculi (columns of Goll and Burdach) are fully developed and well marked.

The white matter of the cord is arranged in tracts or fasciculi. Sometimes these are well marked off by septa. At other times the fasciculi intermingle their fibres, or their edges are ill defined. To understand these fasciculi the functions of the fibres help. Sensory nerves enter the cord and behave differently, according to their function. The nerves for muscle sense, etc. (the kinæsthetic nerves), turn, in the main, upwards in the gracile and cuneate fasciculi. In the gracile fasciculus are found nerves from the sacral and lumbar roots together with the fifth to twelfth thoracic roots. In the cuneate fasciculus are found first to fourth thoracic and the cervical nerves. But these nerves also make connexions at their own level by means of collaterals, and *in addition descend for a segment or two*. We have thus in the gracile and cuneate columns nerve fibres mainly ascending, but a few, in a special interfascicular fasciculus, descending for a segment. This fasciculus is known by many names, of which the most usual is the "comma tract."

The remainder of the white matter of the cord has fibres running in both directions. The sensory ascend and the motor descend.

The other sensory nerves either make their synapses (or connexions) at once, or pass up the cord a segment or so and then do so, around cells in the posterior column. These cells send axons to the *other* side of the cord which pass up superficially in the antero-lateral position. Their termination is in the optic thalamus, and therefore this fasciculus is called the spino-thalamic fasciculus. Some pass up more in the anterior region, and so are called the fasciculus spino-thalamicus anterior. In addition, fibres from nerve cells in the posterior column (which are played upon by sensory impulses) have to make connexions with the cerebellum and the region of the colliculi of the mid brain. (A functional explanation is that when a stimulus giving rise to pain occurs, e.g. a bite in the foot, the cerebellum must aid you in your altered balance, and your eye movements be affected by the mid brain.) Those to the cerebellum run in two divisions: (1) the posterior spino-cerebellar fasciculus, and (2) the anterior spino-cerebellar fasciculus. The former lies on the outer edge of the cord, extending roughly from the three or nine o'clock position

up to the entrance of the posterior root fibres; the latter continues the same circle back from the three o'clock position to five o'clock, or from nine back to seven. The posterior spino-cerebellar fasciculus arises from the nerve cells of the thoracic (dorsal) nucleus *of the same side*; the anterior from a similar nucleus in the sacral and high cervical regions. Other names for these tracts are the direct cerebellar tract of Flechsig, and the indirect cerebellar tract of Gowers.

Extending, then, around from the posterior roots along the margin of the cord are *ascending* tracts in the following order: Fasciculus spino-cerebellaris posterior, fasciculus spino-cerebellaris anterior, fasciculus spino-thalamicus posterior, fasciculus spinotectalis and fasciculus spino-thalamicus anterior. Immediately internal to these ascending tracts are the descending tracts. These are, starting from the right posterior column (see diagram) and moving clockwise, or from the left and moving anti-clockwise: (1) the posterior cerebro-spinal fasciculus or crossed pyramidal tract, carrying impulses from the motor cortex of the brain down to the motor nerve cells of the anterior column on the same side; (2) the rubro-spinal tract arising in the red nucleus, and having the same objective; (3) the tecto-spinal fasciculus uniting the colliculi and motor nerve cells; (4) the vestibulo-spinal fasciculus, carrying impulses arising from the nucleus of the vestibular branch of the acoustic nerve to motor nerve cells of the cord; (5) the anterior cerebro-spinal fasciculus, or uncrossed pyramidal tract. These last fibres do not cross the middle line at the main motor decussation in the medulla oblongata, but postpone their crossing until they reach the spinal cord. Their destination is the same. The functional meaning of these tracts is:

(i) The cerebro-spinal fasciculus. Impulses originating in the motor cortex of the cerebral hemispheres, and concerned in "voluntary" muscle contraction, have to make their way to motor nerve cells in the anterior columns of the cord. The cerebro-spinal fasciculus or pyramidal tract carries these impulses.

(ii) The rubro-spinal fasciculus. The red nucleus is concerned in some way with the tonus of the skeletal muscles. Probably this fasciculus carries the impulses.

(iii) The tecto-spinal fasciculus. The nuclei of the colliculi (corpora quadrigenina) receive impulses from the sensory organs of hearing and vision. Such impulses pre-eminently

lead to alterations of muscle tone and position, e.g. you start when you hear a loud noise. The tecto-spinal tract possibly serves as a short cut to the motor nerve cells.

(iv) The vestibulo-spinal fasciculus. The vestibular branch of the acoustic nerve is concerned with impulses arising from one's position or movements in space. These notoriously influence balance. A man with disturbed semicircular canals or disease of the nerves from them staggers in his gait. The vestibulo-spinal fasciculus makes the connexion between the vestibular nucleus and the motor cells in the spinal cord.

All the area not yet appropriated by ascending or descending tracts consists of fibres running both up and down, and having their origin and endings in the grey matter of the spinal cord. They link different levels of the spinal cord and are termed the fasciculi proprii or ground bundles of the cord. Their function is the co-ordination of activities of different segments of the spinal cord.

In the high cervical region the cord becomes more circular, and rather closely imitates the mid-thoracic region, even to the possession of a lateral column. But it can easily be distinguished: (1) by the large amount of white matter; (2) by the possession of completely formed gracile and cuneate fasciculi; and (3) by the large extent of the formation reticularis in which fibres of the accessory nerve can be seen.

Immediately above this, as we enter the medulla oblongata, a striking rearrangement of parts and development of new structures begin. The cerebro-spinal fasciculi which run in the brain on the side on which they originate cross for the most part to the opposite side low in the medulla oblongata. This is therefore called the region of the *motor decussation.* From fig. 209 (low motor decussation) it will be seen that the section at this level is approximately circular, the central canal has moved (and will continue to move farther) towards the posterior surface, that some fasciculi (e.g. the gracile, cuneate and cerebro-spinal) bulge the exterior of the cord and form funiculi (i.e. little ropes), and that the grey matter has altered in appearance. The alterations comprise:

(i) The appearance of two nuclei—i.e. groups of nerve cells in the gracile and cuneate fasciculi. These are called the gracile and cuneate (i.e. "slender" and "wedge-shaped") nuclei respectively. Passing from below upwards the gracile is the first to develop. In these nuclei are nerve cells around

which the fibres of the cells of the sensory ganglia arborize. This is the first relay station on the tracts concerned with sense of movement of trunk and limbs.

(ii) The return of the posterior column and the substantia gelatinosa to the cabbage appearance of the lumbo-sacral region.

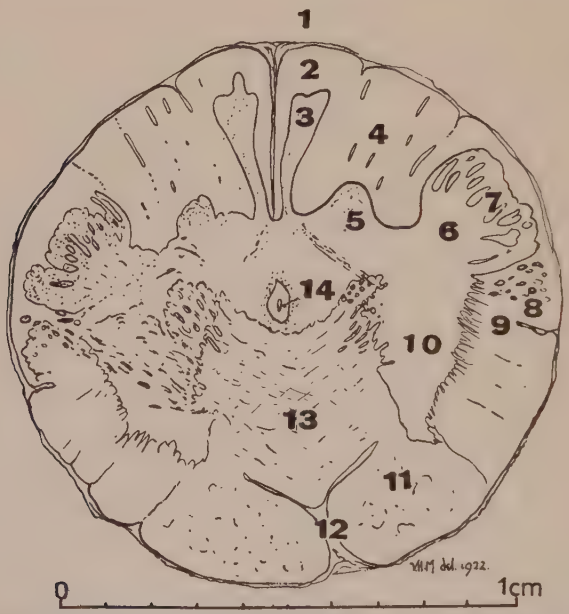



FIG. 209.—Transverse section of the medulla oblongata in the decussation of the cerebro-spinal fasciculus (pyramidal tract). × 6. G.A.H.

(Numerical order.)

1. Posterior median sulcus and septum. 2. Fasciculus gracilis. 3. Nucleus gracilis. 4. Fasciculus cuneatus. 5. Nucleus cuneatus. 6. Posterior column. 7. Substantia gelatinosa of Rolando, immediately external to which is the spinal tract of the trigeminal nerve. 8. Spino-cerebellar tract or direct cerebellar tract of Flechsig. 9. Region of the crossed cerebro-spinal fasciculus (pyramidal tract). 10. Anterior column. 11. Uncrossed cerebro-spinal fasciculus. 12. Anterior median fissure. 13. Fibres of the cerebro-spinal fasciculus crossing from the region of 11 to the opposite side to a position symmetrical with 9. 14. Central canal and surrounding grey matter.

(Alphabetical order.)

Anterior column, 10. Anterior median fissure, 12. Burdach's column, 4. Central canal, 14. Cerebro-spinal fasciculus, crossed, 9. Cerebro-spinal fasciculus crossing, 13. Cerebro-spinal fasciculus, uncrossed, 11. Cuneatus, fasciculus, 4. Cuneatus, nucleus, 5. Direct cerebellar tract of Flechsig, 8. Goll's column, 2. Gracilis, fasciculus, 2. Gracilis, nucleus, 3. Posterior column, 6. Posterior median sulcus and septum, 1. Pyramidal tract, 9. Spino-cerebellar tract, 8. Substantia gelatinosa of Rolando, 7. Trigeminal nerve, spinal tract of, 7.

(iii) The separation of the anterior column from the rest of the grey matter, by white fibres passing across from one side of the cord to the other. In fig. 209 it is complete on the right and incomplete on the left.

In the white matter we observe that :

(i) In the gracile and cuneate fasciculi there is an invasion by grey matter, which, higher up, obliterates these fasciculi. (The fibres of the fasciculi come to an end in arborizations round nerve cells of the gracile and cuneate nuclei.)

(ii) A tract begins to appear close outside the substantia gelatinosa. This is the descending root (tractus spinalis) of the sensory portion of the trigeminal nerve, and is of the same nature as the comma tract in the spinal cord. The descending collaterals of this nerve pass an amazing way down in the central nervous system. The collaterals enter and arborize around nerve cells in the substantia, which therefore may here be called the sensory nucleus of the trigeminal nerve.

(iii) Just anterior to this tract may be seen the spino-cerebellar fasciculus, more obvious than it was in the cord.

(iv) Fibres are passing across from the seven o'clock position to the three o'clock, or from five o'clock to nine o'clock. These are the fibres of the cerebro-spinal fasciculi taking up the position in which we see the " crossed " fibres in the spinal cord, and leaving their old position in the medulla. This crossing is termed the motor decussation.

One other characteristic which we observe is that the anterior fissure may present rather bizarre appearances. It may be Y-shaped or bend to one or other side according to the way the decussation is proceeding. It is rarely symmetrical.

A little above this (fig. 210) the appearance is much the same, but the area of cross section is greater, the gracile and cuneate nuclei have encroached on their respective fasciculi, the spinal tract of the trigeminal nerve is more obvious, and the cerebro-spinal fasciculi are uncrossed. In the grey matter round the central canal groups of nerve cells are obvious. These are the nuclei of the hypoglossal and the accessory nerves. Their fibres may be seen emerging : the hypoglossal along the outer margin of the cerebro-spinal fasciculi and the accessory nerves anterior to the sensory nucleus of the trigeminal nerve. Close beside the emerging fibres of the hypoglossal nerve is seen a small mass of grey matter, outpost of a very important landmark higher. This is an accessory nucleus of the inferior olivary nucleus. Finally, we have the decussation of the lemnisci or fillets beginning. This is sometimes termed the sensory decussation. Nerve cells in the gracile and cuneate nuclei send out projection fibres, the internal arcuate,

which sweep parallel to the grey matter around the central canal, decussate in the middle line with symmetrical fibres from the opposite side and turn upwards in a wedge-shaped

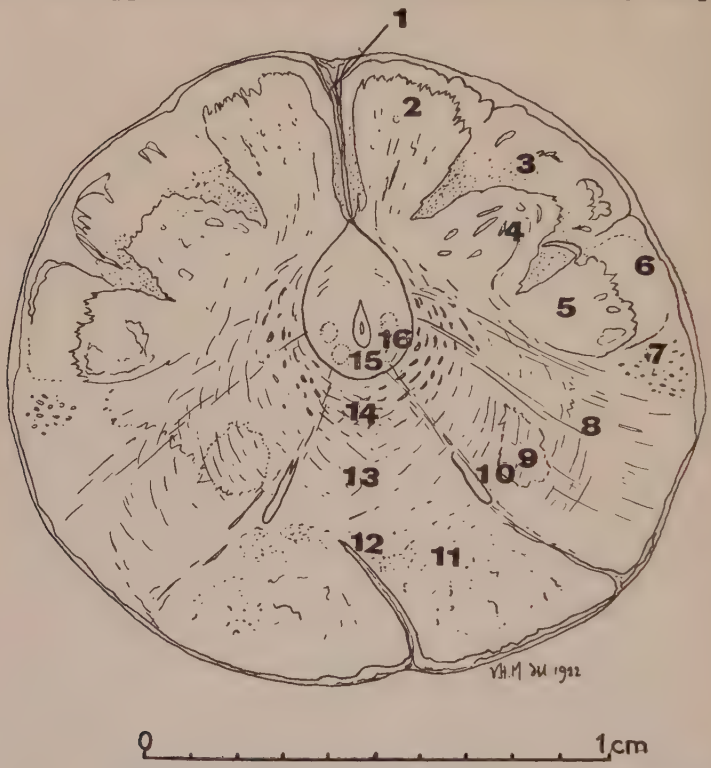



FIG. 210.—Transverse section of the medulla oblongata at the highest level of the motor (cerebro-spinal fascicular or pyramidal) decussation and low in the decussation of the lemniscus (sensory decussation). × 6·2. G.A.H.

(Numerical order.)

1. Posterior median fissure. 2. Nucleus gracilis. 3. Fasciculus cuneatus with accessory nuclei. 4. Main nucleus cuneatus. 5. Posterior column capped with substantia gelatinosa of Rolando. 6. Spinal tract of the trigeminal nerve. 7. Spino-cerebellar spinal fasciculus (direct cerebellar tract of Flechsig). 8. Emerging fibres of the accessory nerve (eleventh cranial nerve). 9. Anterior column. 10. Accessory olivary nucleus. 11. Cerebro-spinal fasciculus (pyramidal tract). 12. Anterior median fissure. 13. Motor decussation. 14. Sensory fibres passing (mainly) from the nucleus gracilis across to the opposite side to form the lemniscus (or fillet). 15. Central canal with its accompanying grey matter. 16. Nucleus of hypoglossal nerve with fibres emerging and leaving the medulla oblongata just lateral to the cerebro-spinal fasciculus (pyramidal tract).

(Alphabetical order.)

Accessory nerve, emerging fibres of, 8. Anterior column, 9. Anterior median fissure, 12. Burdach's column, 3. Central canal, 15. Cerebro-spinal fasciculus, 11. Cuneatus, fasciculus, 3. Cuneatus, main nucleus, 4. Direct cerebellar tract of Flechsig, 7. Gracilis, nucleus, 2. Hypoglossal nerve, nucleus of, 16. Motor decussation, 13. Olivary nucleus, accessory, 10. Posterior column and substantia gelatinosa of Rolando, 5. Posterior median fissure, 1. Pyramidal tract, 11. Sensory decussation, 14. Spino-cerebellar fasciculus, 7. Substantia gelatinosa of Rolando, 5. Trigeminal nerve, spinal tract of, 6.

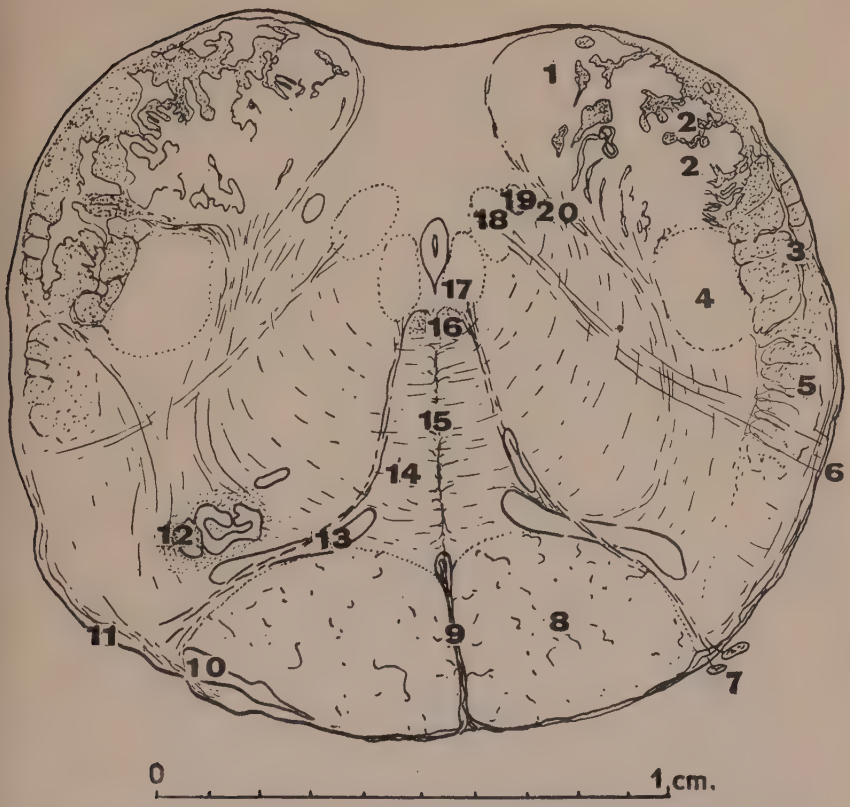



FIG. 211.—Transverse section of the medulla oblongata at the lowest level at which the main olivary nucleus appears. × 6·8. G.A.H.

(Numerical order.)

1. Nucleus gracilis. 2. Nucleus cuneatus. 3. Spinal tract of the trigeminal nerve. 4. Nucleus of trigeminal nerve (substantia gelatinosa of Rolando). 5. Spino-cerebellar fasciculus (direct cerebellar tract of Flechsig). 6. Emerging fibres of the accessory (eleventh) nerve. 7. Emerging fibres and rootlets of the hypoglossal (twelfth) nerve. 8. Cerebro-spinal fasciculus (pyramidal tract). 9. Anterior median fissure. 10. Nucleus of the external arcuate fibres. 11. External arcuate fibres. 12. Main olivary nucleus. 13. Accessory olivary nucleus. 14. Medial lemniscus (or fillet). 15. Raphe. 16. Medial longitudinal fasciculus (posterior longitudinal bundle). 17. Nucleus of the hypoglossal (twelfth) nerve. 18. Nucleus of the vagus and accessory nerves (tenth and eleventh). 19. Fasciculus solitarius (solitary bundle). 20. Internal arcuate fibres.

(Alphabetical order.)

Accessory and vagus nerves, nucleus of, 18. Accessory nerve, emerging fibres of, 6. Anterior median fissure, 9. Cerebro-spinal fasciculus, 8. Cuneate nucleus, 2. Direct cerebellar tract, 5. External arcuate fibres, 11. External arcuate fibres, nucleus of, 10. Fillet, medial, 14. Gracilis, nucleus, 1. Hypoglossal nerve, emerging fibres and rootlets of, 7. Hypoglossal nerve nucleus, 17. Internal arcuate fibres, 20. Lemniscus, medial, 14. Medial longitudinal fasciculus, 16. Olivary nucleus, accessory, 13. Olivary nucleus, main, 12. Posterior longitudinal bundle, 16. Pyramidal tract, 8. Raphe, 15. Solitarius, fasciculus, 19. Substantia gelatinosa of Rolando, 4. Trigeminal nerve nucleus, 4. Trigeminal nerve, spinal tract of, 3. Vagus and accessory nerve nucleus, 18.

area known as the lemniscus or fillet. In fig. 210 the decussation of the lemnisci has but just begun, in fig. 211 it is well developed.

Fig. 211 shows, in addition, an almost complete usurpation of the gracile and cuneate fasciculi by their respective nuclei, a great development of the spinal tract of the trigeminal nerve and its nucleus (3 and 4); the appearance of the main mass of the inferior olivary nucleus on the left side; a well-formed median line or raphe between the lemnisci, and, beside the vago-glosso-pharyngeal nucleus (18), a descending tract, or solitary bundle (19), which consists of collaterals of sensory nerve fibres of the vagus and glosso-pharyngeal nerves. At the apex of the fillets is found a well-marked bundle, the medial longitudinal fasciculus (posterior longitudinal bundle), of which we shall speak more fully later. Between this and the sensory fillet is found the tecto-spinal and spino-tectal tract. Further, we see external arcuate fibres, which arise from cell stations in the gracile and cuneate nuclei, pass across to the raphe, then mainly anteriorly around, but partly behind, the cerebro-spinal fasciculus on the opposite side, and then along the surface of the medulla, finally passing into the restiform body or inferior peduncle of the cerebellum. A nucleus of grey matter, called the arcuate nucleus, is found on their path (10 and 11, fig. 211). It has no connexion with the external arcuate fibres arising from the gracile and cuneate nuclei. Probably its cells receive dendrons from the cerebro-spinal tract, and give rise to axons which pass with the external arcuate fibres up to the cerebellum.

Above this point (fig. 212) the central canal opens out into the fourth ventricle, and the inferior olivary nucleus becomes a conspicuous figure. Further, the development of the restiform body begins. Otherwise, the general arrangement is similar.

The *inferior olivary nucleus* is an isolated mass of grey matter which produces a swelling on the exterior of the medulla known as the olive. The nucleus in transverse section presents a wavy contour incomplete towards the medial aspect. This open slit is called the hilus. There are two flat accessory nuclei of the olive, medial and dorsal. The olive receives nerve fibres from a tract called the thalamo-olivary fasciculus (see later figures), though its thalamic origin has been denied. Possibly there is a spinal afferent path to the olive as well.

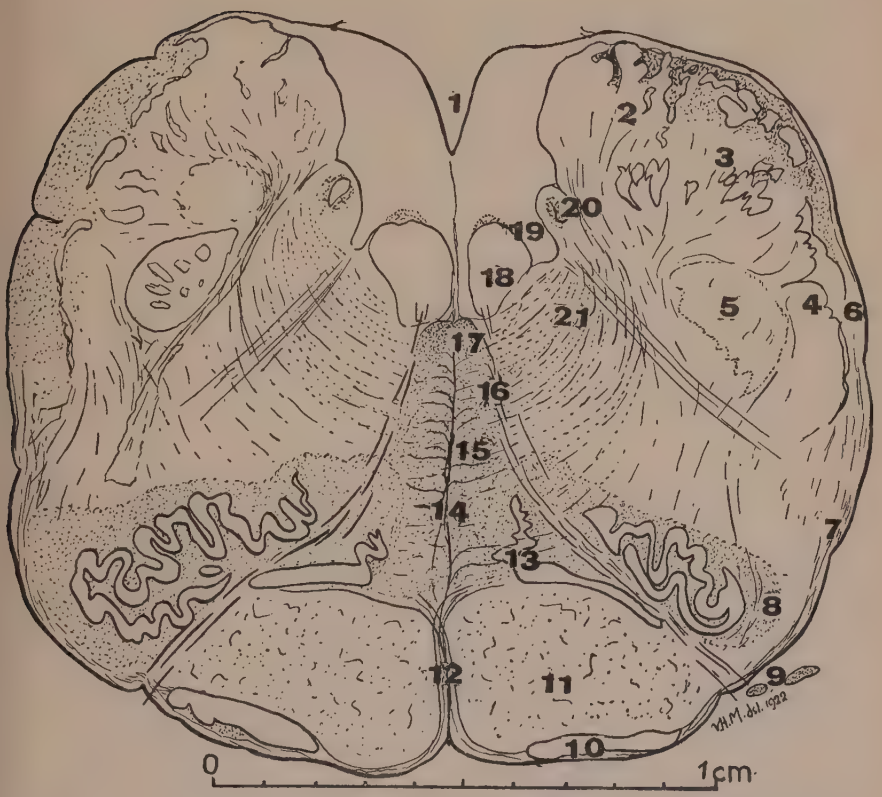



FIG. 212.—Transverse section of the medulla oblongata at the lower end of the fourth ventricle. × 6·7. G.A.H.

(Numerical order.)

1. Fourth ventricle. 2. Nucleus gracilis. 3. Nucleus cuneatus. 4. Spinal tract of trigeminal (fifth) nerve. 5. Nucleus of the root of trigeminal (fifth nerve). 6. Spino-cerebellar fasciculus (direct cerebellar tract by Flechsig). 7. External arcuate fibres. 8. Olivary nucleus. 9. Fibres of the hypoglossal (twelfth) emerging and two hypoglossal rootlets in transverse section. 10. Arcuate nucleus. 11. Cerebro-spinal fasciculus (pyramidal tract). 12. Anterior median fissure and external arcuate fibres. 13. Accessory olivary nucleus. 14. Raphe. 15. Medial lemniscus (or fillet). 16. Fibres of the hypoglossal (twelfth) nerve. 17. Medial longitudinal fasciculus (posterior longitudinal bundle). 18. Nucleus of the hypoglossal (twelfth) nerve. 19. Nucleus of the accessory and vagus (eleventh and tenth) nerves. 20. Solitary bundle. 21. Internal arcuate fibres.

(Alphabetical order.)

Accessory and vagus nerves, nucleus of, 19. Anterior median fissure, 12. Arcuate nucleus, 10. Cerebro-spinal fasciculus, 11. Cuneate nucleus, 3. External arcuate fibres, 7 and 12. Fillet, medial, 15. Fourth ventricle, 1. Gracile nucleus, 2. Hypoglossal nerve fibres emerging, 16. Hypoglossal nerve rootlets, 9. Hypoglossal nucleus, 18. Internal arcuate fibres, 21. Lemniscus, medial, 15. Medial longitudinal fasciculus, 17. Olivary nucleus, 8. Olivary nucleus, accessory, 13. Posterior longitudinal bundle, 17. Pyramidal tract, 11. Raphe, 14. Solitary bundle, 20. Spino-cerebellar fasciculus, 6. Trigeminal nucleus, 5. Trigeminal nerve, spinal tract of, 4. Vagus and accessory nerve nucleus, 19.

Efferent fibres are easy to make out, especially in sections higher than fig. 212. They arise from cells on (say) the left side, pass out through the hilus, and either pierce the nucleus on the opposite side or sweep round it and pass into the restiform body on its internal aspect, and so on to the cerebellum. This fasciculus is termed the olivo-cerebellar fasciculus. It can be seen to separate the nucleus of the spinal tract of the trigeminal nerve from its descending fibres, and to break the latter up into small bundles.

The restiform body begins in this region. It consists of a thin layer of fibres external to the gracile and cuneate nuclei, and immediately under the pia mater. In fig. 212 it is already easily distinguishable on the left side, but not on the right. The restiform body consists of tracts of fibres of various origins, with ultimate destination the cerebellum. These tracts are:

(i) The spino-cerebellar fasciculus or direct cerebellar tract of Flechsig (see figs. 209 and 210 and previous description of spinal fasciculi), arising from cells of the thoracic (or dorsal) nucleus of the grey matter of the spinal cord of the same side.

(ii) The olivo-cerebellar fasciculus, just described, coming from the opposite olive.

(iii) The external arcuate fibres from the gracile and cuneate nuclei of the opposite, together with those arising from the arcuate nuclei apparently of the same side.

(iv) The posterior arcuate fibres. These arise on the external surface of the gracile and cuneate nuclei from cells in those nuclei, and pass to the restiform body of the same side. They are to be seen in fig. 213 on the left side.

The functions of these tracts are to carry proprioceptive[1] impulses from the trunk and limbs to the cerebellum, and to correlate cortical and thalamic activities with those of the cerebellum. Hence the connexions with the inferior olives and the arcuate nuclei.

In fig. 214 two new appearances become obvious, otherwise the ground plan is the same. The restiform body is more complete (5), the spinal tract (7) and nucleus (9) of the trigeminal nerve are conspicuous, and the medial lemniscus, the inferior olivary nucleus, raphe and cerebro-spinal fasciculus

[1] This term is used of those sensory impulses which arise from the activity of the animal itself (e.g. contractions of the muscles), and not directly as the result of a change in the environment.

are all much as before. The new appearances are : (1) a mass of grey matter penetrated in its lateral half by bundles of fibres passing vertically downwards (2 and 3, fig. 214), and

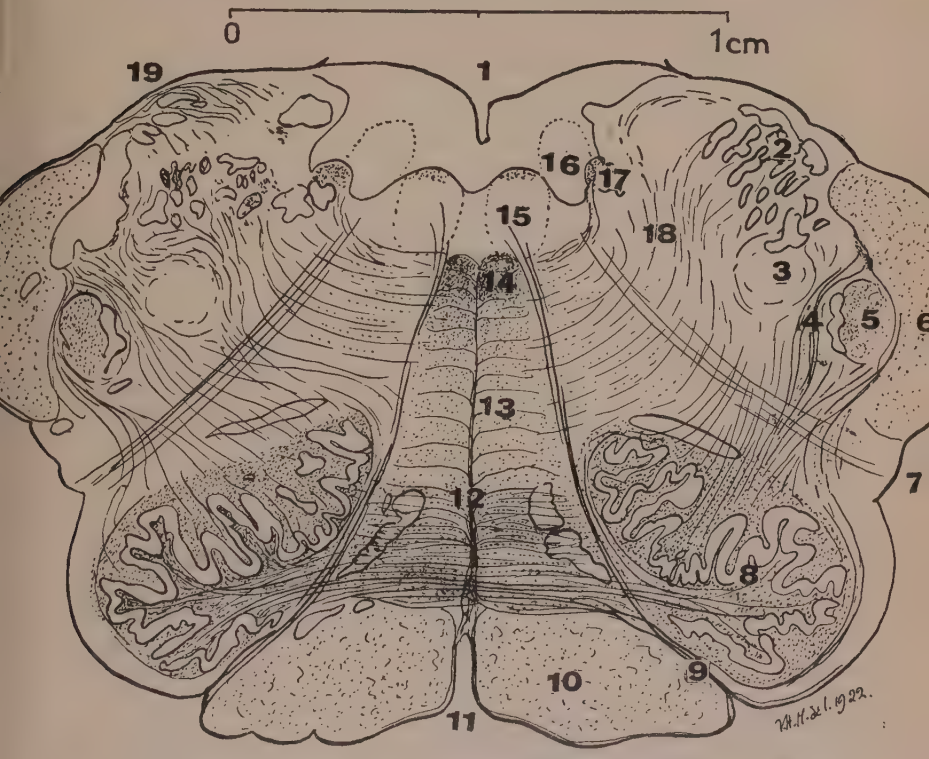



FIG. 213.—Transverse section of the medulla oblongata low in the formation of the restiform body. × 6·5. G.A.H.

(Numerical order.)

1. Fourth ventricle. 2. Nuclei of the posterior fasciculi (gracilis and cuneatus). 3. Nucleus of spinal root of the trigeminal (fifth) nerve. 4. Olivo-cerebellar fibres separating the nucleus of the trigeminal from its spinal tract. 5. Spinal tract of the trigeminal nerve. 6. Restiform body. 7. Emerging fibres of the accessory (eleventh) nerve. 8. Olivary nucleus. 9. Emerging fibres of the hypoglossal (twelfth) nerve. 10. Cerebro-spinal fasciculus (pyramidal tract), with external arcuate fibres on its surface. 11. Anterior median fissure. 12. Raphe. 13. Medial lemniscus (fillet). 14. Medial longitudinal fasciculus (posterior longitudinal bundle). 15. Nucleus of hypoglossal (twelfth) nerve. 16. Main vagus nucleus. 17. Solitary fasciculus and its nucleus. 18. Internal arcuate fibres. 19. Posterior external arcuate fibres.

(Alphabetical order.)

Accessory nerve, emerging fibres of, 7. Anterior median fissure, 11. Cerebro-spinal fasciculus, 10. External arcuate fibres, posterior, 19. External arcuate fibres, anterior, on surface of, 10. Fillet, medial, 13. Fourth ventricle, 1. Hypoglossal nerve, emerging fibres of, 9. Hypoglossal nucleus, 15. Internal arcuate fibres, 18. Lemniscus, medial, 13. Medial longitudinal fasciculus, 14. Olivary nucleus, 8. Olivo-cerebellar fibres, 4. Posterior fasciculi (gracile and cuneate) nuclei, 2. Posterior longitudinal bundle, 14. Raphe, 12. Restiform body, 6. Solitary fasciculus and its nucleus, 16. Trigeminal nucleus, 3. Trigeminal nerve, spinal tract of, 5. Vagus and accessory nerve nucleus, 16.

(2) a large emerging nerve whose fibres arise from the various vago-glosso-pharyngeal nuclei, and pass between the spinal tract of the trigeminal nerve and the restiform body (6, fig. 124).

The grey matter contains two nuclei connected with the vestibular half of the acoustic nerve, and the fibres passing downwards are collaterals of the vestibular nerve fibres. The latter behave just as do the fibres of the trigeminal nerve and the sensory parts of the glosso-pharyngeal nerves. The nuclei are termed the dorsal or principal vestibular nucleus and the lateral nucleus (Deiters).

Emerging in all the sections of the medulla will be seen two main strands of fibres or nerve roots. The first arises from a nucleus close to the central line, and passes eventually outwards between the cerebro-spinal fasciculus and the olives. These fibres are the hypoglossal nerve roots. The nucleus is a long one extending throughout the whole length of the medulla, and the functions of the nerve are purely motor to the tongue. Emerging more laterally is a second group of fibres. These arise from or terminate in a group of nuclei belonging to the accessory nerve and the vagus and glosso-pharyngeal nerves. Three nuclei are to be made out:

(i) The nucleus ambiguus. This is a vague nucleus corresponding to the grey matter of the anterior column of the spinal cord (fig. 214, 10). The cells are large and stellate and are motor in function. Its position is approximately half-way between the nucleus of the spinal tract of the trigeminal nerve and the dorsal accessory nucleus of the inferior olive. The fibres pass dorsally towards the floor of the fourth ventricle, loop around, and then emerge on the ventral side of the spinal tract of the trigeminal if belonging to the accessory nerve, but on the dorsal side if belonging to the vagus. They innervate striped muscle, and so the nucleus ambiguus may be termed the *somatic* nucleus of the group of nerves under consideration.

(ii) The dorsal nucleus (fig. 214, 19). This nucleus is situate laterally and dorsally to the hypoglossal nucleus—more laterally when the fourth ventricle has opened out. It is a mixed nucleus and contains small cells of the visceromotor type, and also cells around which sensory fibres of the vagus and glosso-pharyngeal end. This nucleus is an obvious structure throughout the medulla oblongata except in its lowest limits, and so is almost as long as the hypoglossal. It

is the splanchnic nucleus of the vago-glosso-pharyngeal group.

(iii) The nucleus of the solitary fasciculus (fig. 214, 4). Grey matter closely accompanies the solitary bundle throughout its length. Fibres mainly of the sensory branch of the

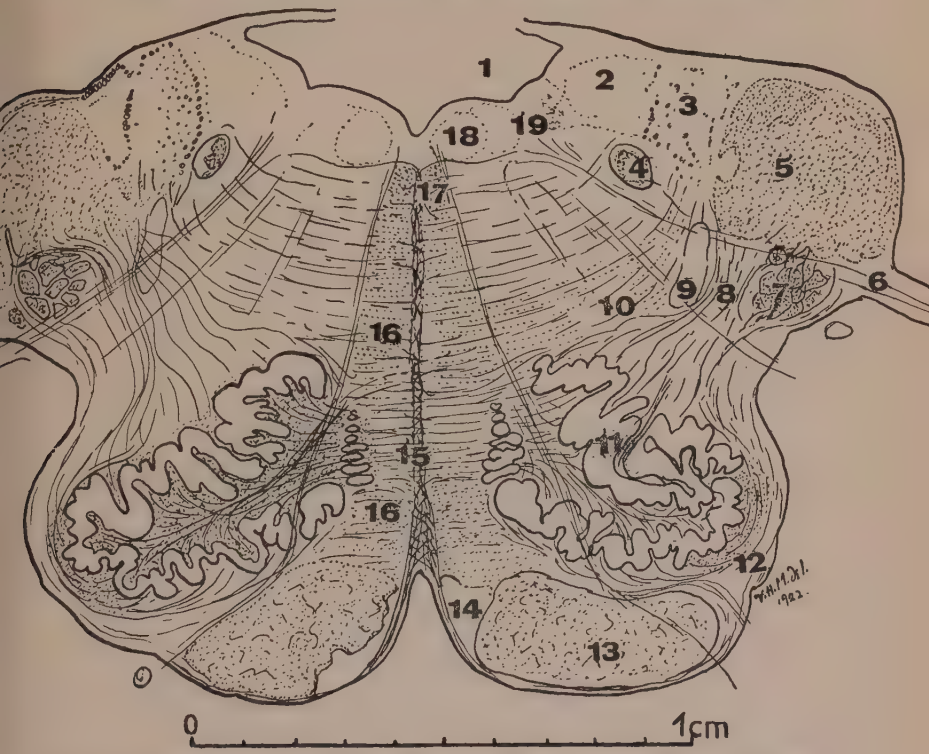



FIG. 214.—Transverse section of the medulla oblongata in the region of the origin of the vagus (tenth) nerve. × 6·6. G.A.H.

(Numerical order.)

1. Fourth ventricle. 2. Medial vestibular nucleus. 3. Lateral vestibular nucleus (Deiters') and descending root of the vestibular nerve. 4. Fasciculus solitarius (solitary bundle) and nucleus. 5. Restiform body. 6. Vagus (tenth) nerve. 7. Spinal tract of the trigeminal (fifth) nerve. 8. Olivo-cerebellar fibres. 9. Trigeminal nucleus. 10. Nucleus ambiguus. 11. Inferior olivary nucleus. 12. External arcuate fibres and thalamo-olivary fasciculus. 13. Cerebro-spinal fasciculus (pyramidal tract). 14. Arcuate nucleus. 15. Raphe. 16. Medial lemniscus (fillet). 17. Medial longitudinal fasciculus (posterior longitudinal bundle). 18. Nucleus of the hypoglossal (twelfth) nerve. 19. Dorsal nucleus of the glosso-pharyngeal (ninth) and vagus (tenth) nerves.

(Alphabetical order.)

Ambiguus, nucleus, 10. Arcuate nucleus, 14. Cerebro-spinal fasciculus, 13. Deiters' nucleus, 3. External arcuate fibres, 12. Fillet, medial, 16. Fourth ventricle, 1. Glosso-pharyngeal nerve, dorsal nucleus of, 19. Hypoglossal nucleus, 18. Lemniscus, medial, 16. Medial longitudinal fasciculus, 17. Olivary nucleus, 11. Olivo-cerebellar fibres, 8. Posterior longitudinal bundle, 17. Pyramidal tract, 13. Raphe, 15. Restiform body, 5. Solitary fasciculus and nucleus, 4. Thalamo-olivary fasciculus and external arcuate fibres, 12. Trigeminal nerve, spinal tract of, 7. Trigeminal nucleus, 9. Vagus nerve, 6. Vagus nucleus (dorsal), 19. Vestibular nerve, descending root of, 3. Vestibular nucleus, lateral, 3. Vestibular nucleus, medial, 2.

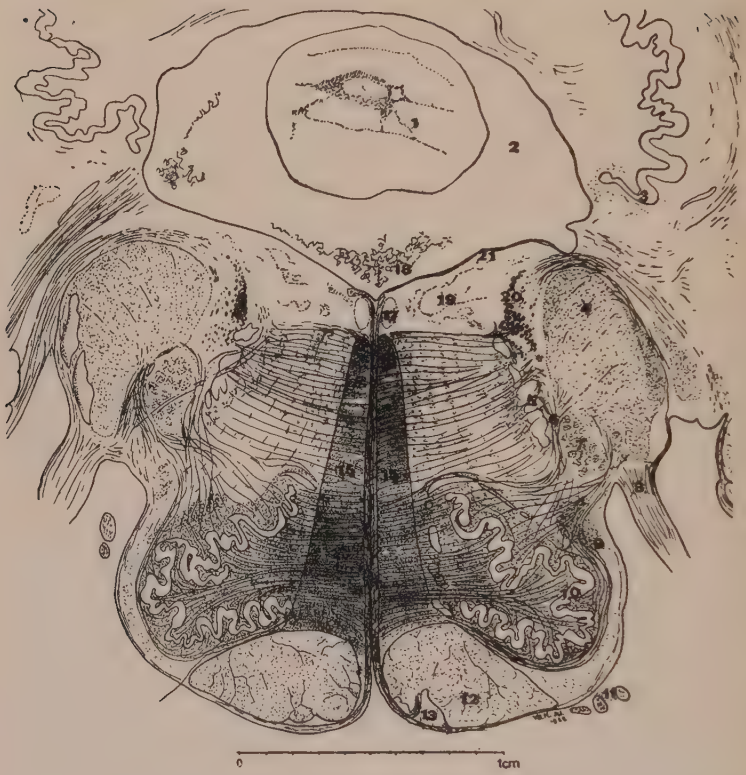



FIG. 215.—Transverse section of the medulla and part of the cerebellum with which it is continuous. Magnified 3·5 times.

(Numerical order.)

1. Nodule of the cerebellum. 2. Fourth ventricle. 3. Nucleus dentatus of the cerebellum. 4. Restiform body. 5. Nucleus of the spinal tract of the trigeminal (fifth) nerve. 6. Olivo-cerebellar fibres. 7. Spinal tract of the trigeminal (fifth) nerve. 8. Acoustic (eighth) nerve. 9. External arcuate fibres and (internally) thalamo-olivary tract. 10. Inferior olivary nucleus. 11. Roots of hypoglossal (twelfth) nerve. 12. Cerebro-spinal fasciculus (pyramidal tract). 13. Arcuate nucleus. 14. Raphe. 15. Medial lemniscus (fillet). 16. Median longitudinal fasciculus (posterior longitudinal bundle). 17. Nucleus of the hypoglossal (twelfth) nerve. 18. Debris of choroid plexus. 19. Grey matter containing nuclei of the glosso-pharyngeal and vestibular branch of the acoustic nerve. 20. Lateral vestibular nucleus (Deiters') and descending roots of the acoustic nerve. 21. Striæ medullares.

(Alphabetical order.)

Acoustic nerve, 8. Acoustic nerve, descending roots of vestibular branch of, 20. Acoustic nerve, nucleus of vestibular branch of, 19. Arcuate nucleus, 13. Cerebellum, nodule of, 1. Cerebro-spinal fasciculus, 12. Choroid plexus, debris of, 18. Deiters' nucleus, 20. Dentate nucleus of cerebellum, 3. External arcuate fibres, 9. Fillet, medial, 15. Fourth ventricle, 2. Glosso-pharyngeal and vestibular nuclei, 19. Hypoglossal nucleus, 17. Hypoglossal nerve, rootlets of, 11. Lemniscus, medial, 15. Medial longitudinal fasciculus, 16. Olivary nucleus (inferior), 10. Olivo-cerebellar fibres, 6. Posterior longitudinal bundle, 16. Pyramidal tract, 12. Raphe, 14. Restiform body, 4. Striæ medullares, 21. Trigeminal nerve, nucleus, 5. Trigeminal nerve, spinal tract of, 7. Thalamo-olivary tract, 9. Vestibular nucleus, lateral, 20.

glosso-pharyngeal, but also of the vagus and sensory root of the facial nerve, run down the solitary bundle and end around nerve cells in the grey matter which accompanies it. Apparently it is the termination of the gustatory nerves.

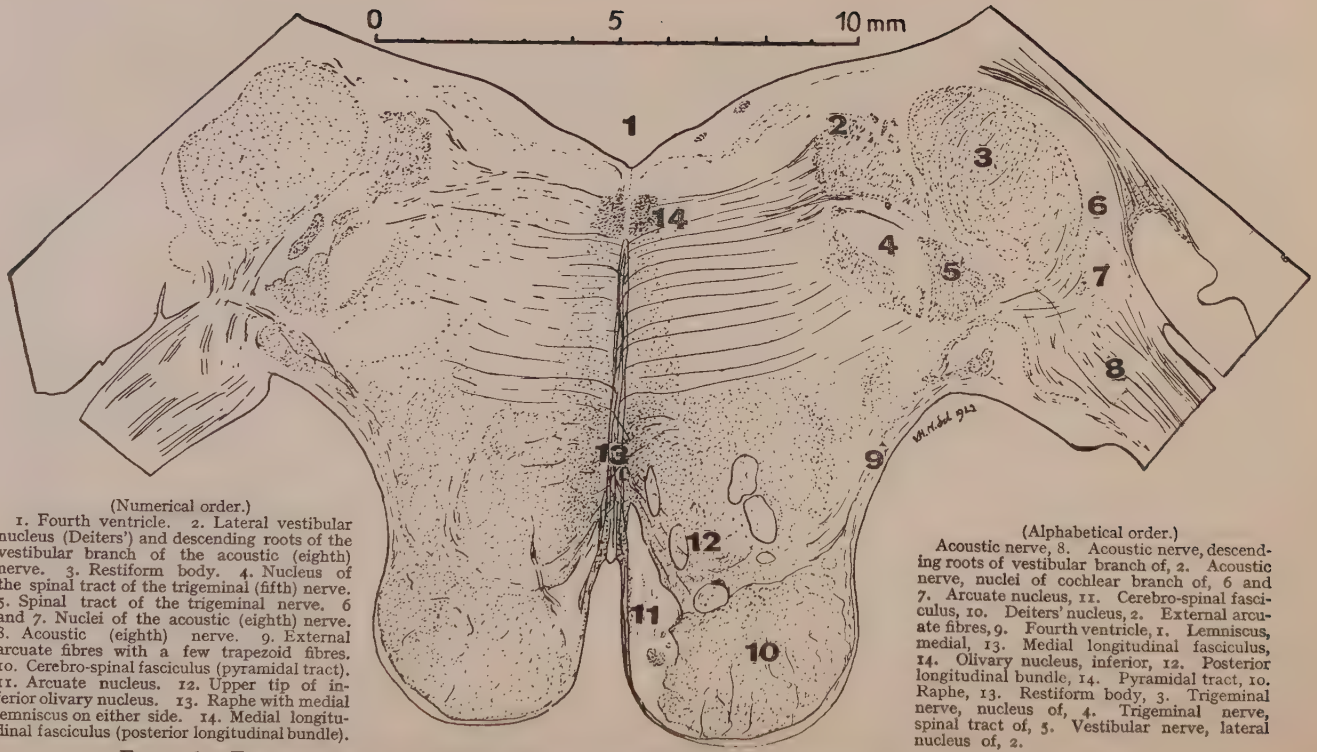
Immediately above this region sections begin to cut through the cerebellum. It is possible, if the section is made rigidly at right angles across the axis of the fourth ventricle, to include a great deal of the cerebellum without touching the pons. Usually, such is the difficulty of preparing sections of the central nervous system, the portions of the cerebellum which would be included in an ideal section, are cut away. The student must be on his guard against assuming that in figs. 215 to 219 the whole of the central nervous system at that section is represented. A varying amount of the cerebellum has been cut away.

Fig. 215 shows a section just below the region of the pons. Above, a considerable proportion of the cerebellum is shown. The whole of the fourth ventricle is included, together with a portion of the cerebellum that pushes down into the fourth ventricle, the nodule. On both sides portions of the nuclei dentati [1] are seen, and below, portions of the flocculi.[2] In the medulla oblongata the general picture is much as before. The nucleus of the hypoglossal is still visible, and a few fibres of the glosso-pharyngeal nerve are emerging on the left, and rootlets in transverse section, which may belong to that nerve or the vagus, are seen. The large entrant nerve is the cochlear branch of the acoustic nerve, with the grey matter of its nuclei at its base and high up on the external aspect of the restiform body. These will be seen better in later figures (216 and 217).

In the next fig. (216) a similar appearance is seen, except that the nucleus of the inferior olive has almost disappeared. A few outlying portions only of it are visible. The acoustic nerve enters, bifurcates and runs on both sides of the restiform body. On the external side there is a nucleus to which it runs : the acoustic tubercle (6). At 7, and also internally to the restiform body, there are accessory nuclei on the internal

[1] The nucleus dentatus is a wavy nucleus of large extent, crinkled like a walnut kernel, found deep in the white matter of each hemisphere of the cerebellum.

[2] The flocculus is a small irregular lobule of the cerebellum, found on the under side, in close proximity to the restiform body and the acoustic nerve.




(Numerical order.)

1. Fourth ventricle. 2. Lateral vestibular nucleus (Deiters') and descending roots of the vestibular branch of the acoustic (eighth) nerve. 3. Restiform body. 4. Nucleus of the spinal tract of the trigeminal (fifth) nerve. 5. Spinal tract of the trigeminal nerve, 6 and 7. Nuclei of the acoustic (eighth) nerve. 8. Acoustic (eighth) nerve. 9. External arcuate fibres with a few trapezoid fibres. 10. Cerebro-spinal fasciculus (pyramidal tract). 11. Arcuate nucleus. 12. Upper tip of inferior olivary nucleus. 13. Raphe with medial lemniscus on either side. 14. Medial longitudinal fasciculus (posterior longitudinal bundle).

(Alphabetical order.)

Acoustic nerve, 8. Acoustic nerve, descending roots of vestibular branch of, 2. Acoustic nerve, nuclei of cochlear branch of, 6 and 7. Arcuate nucleus, 11. Cerebro-spinal fasciculus, 10. Deiters' nucleus, 2. External arcuate fibres, 9. Fourth ventricle, 1. Lemniscus, medial, 13. Medial longitudinal fasciculus, 14. Olivary nucleus, inferior, 12. Posterior longitudinal bundle, 14. Pyramidal tract, 10. Raphe, 13. Restiform body, 3. Trigeminal nerve, nucleus of, 4. Trigeminal nerve, spinal tract of, 5. Vestibular nerve, lateral nucleus of, 2.

FIG. 216.—Transverse section of the medulla oblongata just below the pontine region. (The cerebellum has been cut away above and on both sides of the section.) × 6·4.

branch of the nerve. From the acoustic tubercle or dorsal cochlear nucleus fibres pass around the restiform body and along just under the floor of the fourth ventricle to the middle line. Here they turn inwards and pass to a position lateral to that of the medial lemniscus and close to the main facial nucleus (see fig. 218). Here they join fibres from the trigeminal nucleus and pass upwards as the lateral lemniscus. The striæ they form in their early course across the floor of the fourth ventricle are termed the striæ medullares. From the accessory or ventral cochlear nucleus fibres run in parallel lines transversely across to the opposite side. These fibres are known as the trapezoid body and are more obvious in later sections. When they have reached the neighbourhood of the lateral lemniscus on the opposite side they, too, turn upwards and join the nerves arising from the dorsal nucleus on their way to the thalamus. As the trapezoid fibres pass the superior olivary nucleus (6, fig. 218) they give off collaterals which synapse with cells in the olive, and receive additions from that nucleus. Similarly, too, with the grey matter of the trapezoid body, and again, higher up (fig. 220) in the nucleus of the lateral lemniscus. The cochlear branch of the acoustic nerve has then: (1) main relay stations in the dorsal nucleus or acoustic tubercle and the ventral nucleus; (2) partial relay stations in the superior olivary nucleus, the nucleus of the trapezoid body and the nucleus of the lateral lemniscus; (3) terminal and relay stations in the inferior colliculi (figs. 220 and 221); (4) a relay station in the medial geniculate body (figs. 222 and 223); and (5) representation in the cortex in the transverse temporal gyri.

The vestibular branch of the acoustic nerve enters a little higher than the cochlear branch, and its fibres pass on the internal aspect of the restiform body to the wedge-shaped area of grey matter just under the floor of the fourth ventricle. The fibres bifurcate. Some collaterals pass downwards, as we have already seen, and make their synapses at a lower level than the point of entry; some connect at the same level in the principal nucleus or dorsal vestibular nucleus; and some connect with the lateral nucleus (Deiters' nucleus), or its upper extension, the superior vestibular nucleus (or Becterew's nucleus). Some vestibular fibres pass into the cerebellum without interruption.

The lateral nucleus (Deiters') has projection fibres which

pass to the medial longitudinal bundle (posterior longitudinal bundle). These traverse the central nervous system in both directions and connect the oculo-motor, trochlear and abducent nuclei above with the accessory nerve nucleus, and probably the anterior columns of the spinal cord. Functionally the interpretation of this is that when the part of the ear connected with balance is disturbed movements of the eyes, head, neck and trunk, etc., are required for readjustment. Some fibres pass from the same nucleus direct in the vestibulo-spinal fasciculus to the spinal cord, and some from the superior (Bechterew's) nucleus upwards to the oculo-motor nuclei. The functional interpretation of these facts is clear.

From now on, for a number of sections, we pass into the region of the pons. A functional explanation of this region will help in understanding it. The cerebellum is the great head ganglion of the proprioceptive impulses (Sherrington). Into it are gathered together all the impulses which are set up by the position and movement of the body in space as a whole or by the alteration of the relative position of its parts. Its function is to co-ordinate the adjustments of the body to these proprioceptive influences and to guide the activity of the skeletal muscles. The motor cortex initiates impulses which result in movement. These impulses are carried by the cerebro-spinal fasciculus. It is important that the cerebellum should be made aware of what is about to happen. Fibres from cells in the motor cortex therefore pass down with the cerebro-spinal fasciculus, and end in synapses around cells in the grey matter of the pons in the neighbourhood of the cerebellum. This grey matter (nerve cells) gives rise to nerve fibres which sweep across to the opposite side and pass into the cerebellum. They form the pons.

This accounts for the appearance presented in the pontine region. Take fig. 216, and imagine large numbers of fibres sweeping across from side to side, with considerable grey matter between them, and embedding and breaking up the cerebro-spinal fasciculi. You then have an appearance very similar to that of fig. 217.[1]

[1] Or again. Imagine the external arcuate fibres and the arcuate nuclei very much hypertrophied and imbedding the cerebro-spinal fasciculi and you obtain a similar result. It will be remembered that the functions of the arcuate nuclei and some of the external arcuate fibres are the same as those given above for the transverse fibres of the pons.

Omitting the cerebellum, which has been cut away for the most part, the preparation consists of two parts: (1) the dorsal, which is a continuation upwards of the medulla oblongata, minus the cerebro-spinal fasciculi, and (2) the basilar

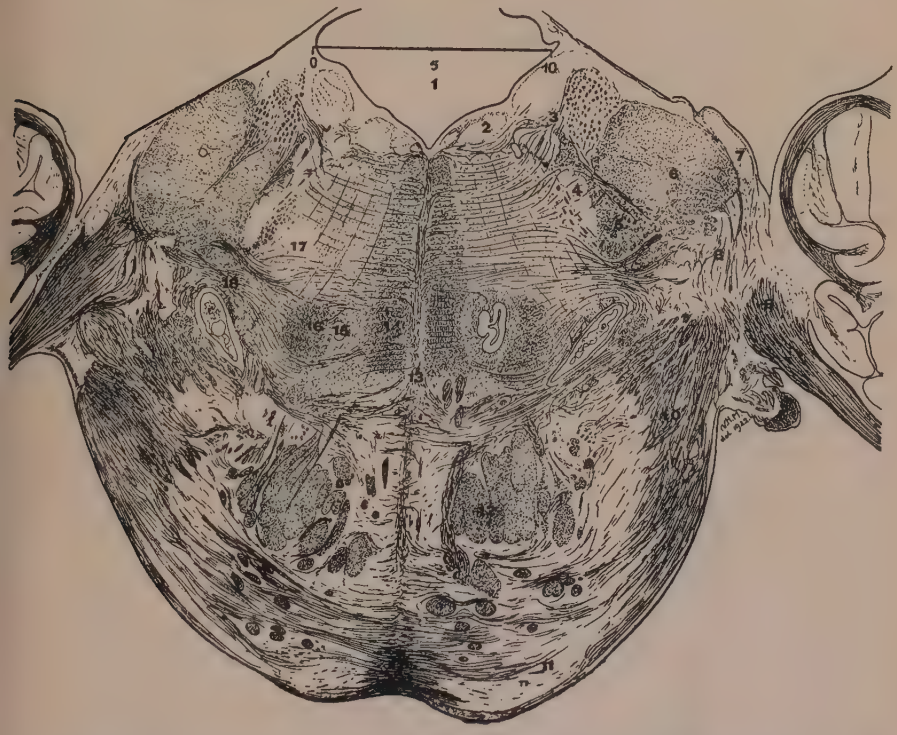



FIG. 217.—Transverse section of the brain stem in the lowermost portion of the pons varolii (the major portion of the cerebellum has been removed). × 3·1.

(Numerical order.)

1. Fourth ventricle. 2. Nucleus of abducens (sixth) nerve. 3. Nuclei of the vestibular part of the acoustic (eighth) nerve. 4. Nucleus of the spinal tract of the trigeminal (fifth) nerve, on the inner aspect of which are emerging fibres of the glosso-pharyngeal (ninth) nerve. 5. Spinal tract of the trigeminal (fifth) nerve. 6. The restiform body. 7. Acoustic tubercle (nucleus of cochlear branch of the acoustic nerve). 8. Nuclei of cochlear nerve. 9. Acoustic (eighth) nerve. 10. Fibres of the pons varolii. 11. Superficial fibres of the pons with grey matter, the nuclei pontis. 12. Cerebro-spinal fasciculus broken up into smaller bundles. 13. Raphe. 14. Medial lemniscus (fillet). 15. Olivary nucleus. 16. Thalamo-olivary tract. 17. Nucleus of facial (seventh) nerve. 18. Trapezoid fibres.

(Alphabetical order.)

Acoustic nerve, 9. Abducens nucleus (main), 2. Acoustic tubercle (one nucleus of cochlear branch). Acoustic nerve, nucleus of vestibular part, 3. Cochlear nerve, nuclei, 8. Cerebro-spinal fasciculus, 12. Facial nerve nucleus, 17. Fillet (medial), 14. Fourth ventricle, 1. Lemniscus, medial, 14. Nuclei pontis, 11. Olivary nucleus (inferior), 15. Pons, superficial fibres, 11. Pons, fibres of, 10. Raphe, 13. Restiform body, 6. Trapezoid fibres, 18. Trigeminal nucleus, 4. Trigeminal nerve, spinal tract of, 5. Thalamo-olivary tract, 16.

part, which consists of: (*a*) longitudinal fibres—the cerebro-spinal and cortico-pontine fasciculi; (*b*) transverse fibres running from grey matter on one side of the pons across the

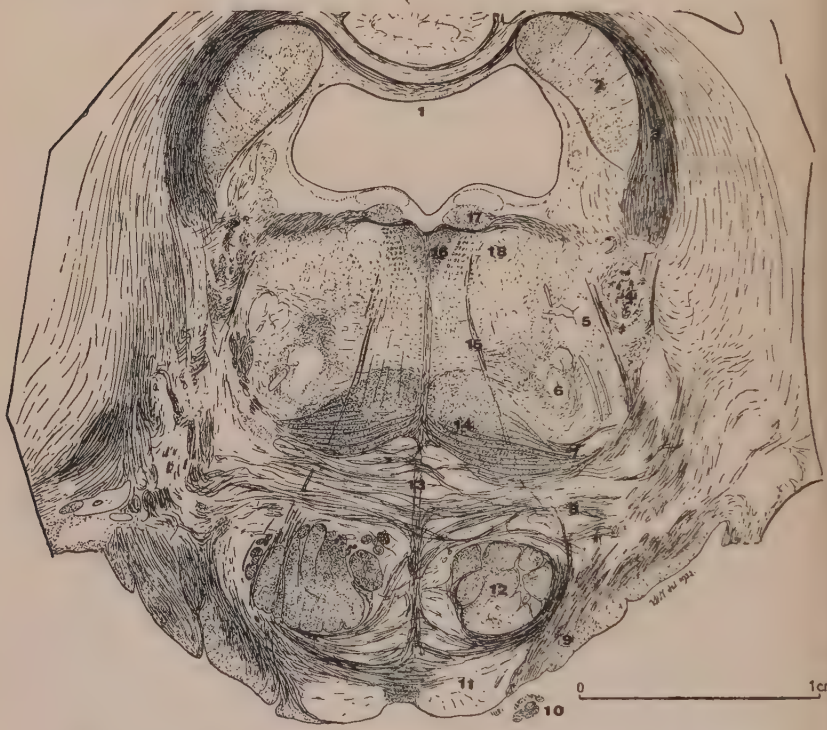



FIG. 218.—Transverse section of the central nervous system in the pontine region at the level of the nuclei of the abducens and facial nerves. (Much of the cerebellum has been cut away.) × 3·2. G.A.H.

(Numerical order.)

1. Fourth ventricle. 2. Brachium conjunctivum (superior peduncle of the cerebellum). 3. Fibres of the restiform body. 4. Spinal tract of trigeminal (fifth) nerve and its nucleus. 5. Nucleus of the facial (seventh) nerve. Passing between 4 and 5 are a few of the facial fibres, on their way outwards after having made a loop around the nucleus of the abducens (sixth) nerve. 6. Nucleus of the superior olive. 7. Trapezoid body. 8. Deep fibres of the pons. 9. Superficial fibres of the pons. 10. Rootlets of the abducens (sixth) nerve. 11. One of the nuclei pontis—grey matter of the pons. 12. Cerebro-spinal fasciculus (pyramidal tract). 13. Raphe. 14. Medial lemniscus (fillet) with lateral fillet forming to its side. 15. Emerging fibres of the abducens (sixth) nerve. 16. Medial longitudinal fasciculus (posterior longitudinal bundle). 17. Genu of the facial (seventh) nerve. 18. Nucleus of the abducens (sixth) nerve.

(Alphabetical order.)

Abducens nerve, emerging fibres, 15. Abducens, main nucleus, 18. Abducens, rootlets of, 10. Brachium conjunctivum, 2. Cerebro-spinal fasciculus, 12. Facial nerve, genu of, 17. Facial nerve, nucleus of, 5. Fillet, medial, 14. Fourth ventricle, 1. Lemniscus, medial, 14. Medial longitudinal fasciculus, 16. Nuclei pontis, one of the, 11. Olivary nucleus, superior, 6. Pons, deep fibres of, 8. Pons, grey matter of, 11. Pons, superficial fibres of, 9. Posterior longitudinal bundle, 16. Raphe, 13. Restiform body, fibres of, 3. Superior peduncle of the cerebellum, 2. Trapezoid body and nucleus, 7. Trigeminal nerve, spinal tract of, and nucleus, 4.

middle line and into the cerebellum on the opposite side, best seen in fig. 218; and (*c*) grey matter scattered between the transverse fibres, but often seen gathered together in large masses, as in figs. 218 and 219.

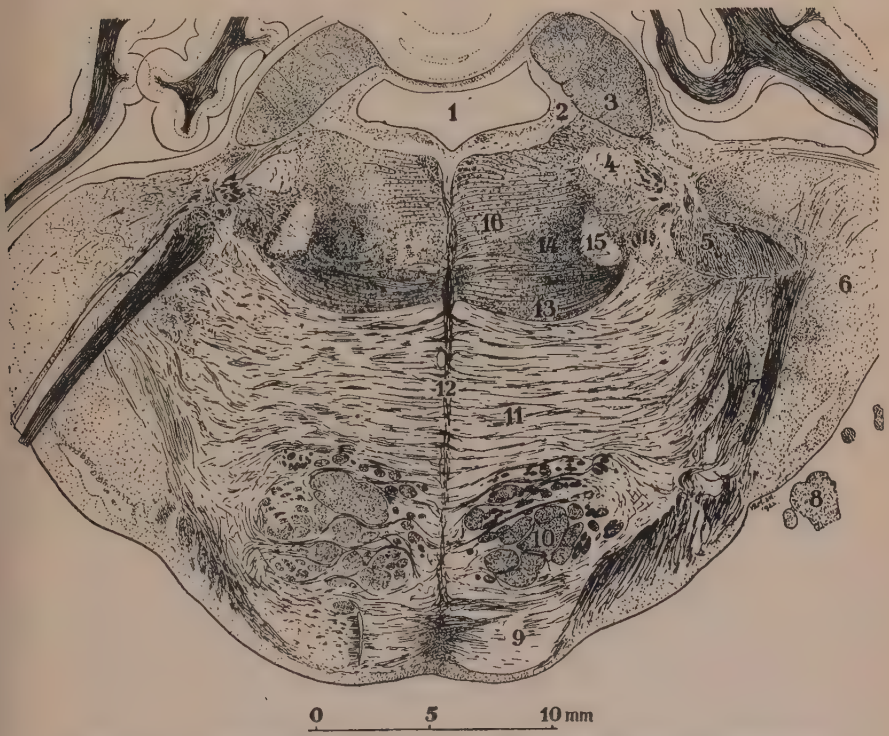



FIG. 219.—Transverse section of the central nervous system in the pontine region at the level of the nucleus of and entrance and exit of the trigeminal (fifth) cranial nerve. (Much of the cerebellum has been cut away.) × 3·2. G.A.H.

(Numerical order.)

1. Fourth ventricle. 2. Accessory motor nucleus of the trigeminal (fifth) nerve. 3. Brachium conjunctivum. 4. Main motor nucleus of trigeminal nerve. 5. Emerging fibres of trigeminal nerve. 6. Brachium of the pons. 7. Pontine fibres cut obliquely. 8. Rootlets of trigeminal nerve. 9. Nucleus pontis, or grey matter of pons. 10. Cerebro-spinal fasciculus (or pyramidal tract). 11. Deeper layers of pontine fibres. 12. Raphe. 13. Lemniscus and fibres of trapezius. 14. Thalamo-olivary tract. 15. Superior olivary nucleus. 16. Scattered grey matter with, immediately to the left and above, the medial longitudinal bundle (posterior longitudinal bundle).

(Alphabetical order.)

Accessory motor nucleus (trigeminal), 2. Brachium conjunctivum, 3. Brachium of pons, 6. Cerebro-spinal fasciculus, 10. Fillet, 13. Fourth ventricle, 1. Lemniscus, 13. Main motor nucleus (trigeminal), 4. Medial longitudinal bundle, above 16 to the left. Nuclei pontis, 9. Olive (superior), 15. Pons. Brachium, 6; deep fibres of, 11; grey matter of, 9 and 11. Posterior longitudinal bundle—above 16 to left. Pyramidal tract, 10. Raphe, 12. Superior olive, 15. Thalamo-olivary tract, 14. Trapezius, 13. Trigeminal nerve. Accessory motor nucleus, 2; emerging fibres, 5; main motor nucleus of, 4; rootlets of, 8.

FIG 220.—Transverse section of the brain stem in the lower part of the mid-brain (region of the inferior colliculus or posterior corpora quadrigemina). × 3·6. G.A.H.

(Numerical order.)

1. Nucleus of inferior colliculus (posterior corpus quadrigeminum). 2. Lateral lemniscus (fillet) and nucleus. 3. Medial lemniscus (fillet). 4. Cerebro-spinal fasciculi (pyramidal tract), together with grey matter of the pons, *4a*, and pontine fibres, *4b*. 5. Decussating fibres of the pons. 6. Decussation of the brachia conjunctiva (superior cerebellar peduncles). 7. Medial longitudinal fasciculus (posterior longitudinal bundle). 8. Cerebral aqueduct (of Sylvius). 9. Trochlear (fourth) nerve. 10. Descending (motor) tract of the trigeminal (fifth) nerve. 11. Brachium conjunctivum (superior cerebellar peduncle). 12. Thalamo-olivary tract.

(Alphabetical order.)

Aqueduct, cerebral, of Sylvius, 8. Brachia conjunctiva, decussation of, 6. Brachium conjunctivum, 11. Cerebro-spinal fasciculus, 4. Colliculus, nucleus of inferior, 1. Fillet, lateral, nucleus of, 2. Fillet, medial, 3. Lemniscus, lateral, 2. Lemniscus medial, 3. Medial longitudinal fasciculus, 7. Pons, decussating fibres of, 5. Pons, grey matter, *4a*, and fibres, *4b*. Posterior corpus quadrigeminum, 1. Posterior longitudinal bundle, 7. Pyramidal tract, 4. Superior cerebellar peduncle, 11. Thalamo-olivary tract, 12. Trigeminal nerve, motor tract of, 10. Trochlear nerve, bundle on the way to emergence, 9.

The longitudinal fibres are seen to consist of two moderately compact bundles lower down (figs. 217 and 218), but higher up they are very considerably broken up (fig. 219), this arrangement persisting even into the region of the inferior colliculi (figs. 220 and 221). There are twice as many fibres in the longitudinal bundles when they enter the pons above, as there are when they emerge below as the cerebro-spinal fasciculus. This is partly explained by the fact that some motor fibres from the cortex of the brain end in the motor nuclei of the trigeminal, abducent and facial nerves situated in the pontine region. But the main reason is that many of the longitudinal fibres run from the cortex to the pons, and synapse around grey matter in the pons—the nuclei pontis. This grey matter is packed in the interstices between longitudinal and transverse fibres. The transverse fibres run both superficially and deeply, completely embedding and interpenetrating the longitudinal bundles. Externally they are gathered together in a dense mass known as the brachium of the pons (fig. 219).

Turning to the dorsal portion of the pons it is convenient to discuss separately three levels: (1) the lowest, in which the acoustic or eighth nerve is still prominent (fig. 217); (2) one a little above, in which the abducent and facial nerves are seen emerging (fig. 218); and (3) one considerably higher in which the entrant and emerging fibres of the trigeminal nerve are present (fig. 219). The medial lemniscus, which of course is common to all three sections, shows an interesting change in position. Instead of being a vertical, wedge-shaped area along the raphe, it begins to turn into a horizontal position parallel with the fibres of the pons. This change of position is complete by the time the entrance of the trigeminal nerve is seen. It is in preparation to pass to its termini later on.

In a section of the pons in which the acoustic nerve is included, we see in the dorsal or tegmental portion most of the structures seen in the upper medulla. The dorsal and lateral nuclei of the vestibular nerve and the descending vestibular tract are still seen, as is also the restiform body and the grey matter of the cochlear nuclei. The trapezial fibres are beginning to develop (fig. 217, 18). The nucleus of and spinal tract of the trigeminal nerve form their usual landmarks. Sometimes the extreme tip of the inferior olive may be seen, with, on its lateral aspect, a dense mass of small

fibres, the thalamo-olivary tract. The lemniscus is still in its vertical position between the raphe and the inferior olivary nucleus. Sometimes the somatic nucleus of the facial nerve may be seen in a position corresponding to the nucleus ambiguus lower down, and sometimes fibres passing in its neighbourhood inwards towards the grey matter of the floor of the fourth ventricle may be seen. These are the fibres of the intermediate nerve or sensory branch of the facial nerve. They cut through the trigeminal nucleus (4, fig. 217), and end in the region of the solitary bundle.

Fig. 218 shows a section at the level of nuclei of the facial and abducent nuclei. We note that the restiform body has gone up to the cerebellum and that its fibres are now cut longitudinally. Internally to it a structure is seen easily mistakable for the restiform body. This is the brachium conjunctivum, or superior cerebellar peduncle, coming from the nucleus dentatus in the cerebellum, and passing upwards towards the mid-brain. If we look at the raphe and choose the median longitudinal fasciculus (posterior longitudinal bundle) we shall see dorsally to it, and a little laterally, a thick bundle of fibres cut transversely. These are fibres of the facial nerve which have arisen from its somatic nucleus, much deeper and more lateral in the tegmentum (5, fig. 218). They have passed inwards and upwards and now bend around and over the nucleus of the abducent nerve (18, fig. 218), and pass out between its nucleus and the trigeminal nucleus and tract. Fibres can be traced into the nucleus from the trigeminal nucleus, from the trapezoid body, and, of course, from the cerebro-spinal fasciculus. The functional significance of all these is fairly obvious—the muscles of the face are influenced by sensory impulses from the skin and the ear, and by motor impulses from the cortex of the brain.

Next in importance is the nucleus of the abducens nerve (sixth). This is found under the crook formed by the facial nerve fibres. From it fibres pass out, penetrate through the lemniscus and trapezium, the pontine fibres, and often between the longitudinal bundles of the pons to the exterior (fig. 218, 10 and 15). Below and internal to the facial nucleus is a mass of grey matter, the superior olivary nucleus. It receives fibres from, and gives fibres to, the trapezoid body, and further fibres pass from it to the nucleus of the abducens, thus giving a short path for auditory impulses to one of the nuclei of the

eye muscles. The medial lemniscus is passing out into its horizontal position, and its lower portion is pierced by the transverse fibres of the trapezium.

In fig. 219 we have a representation of a cross section of the brain, where the roots of the trigeminal (fifth) nerve enter and leave. Again we notice the brachium conjunctivum as a prominent object. On its internal margin are the cells of the ascending root—better, the mesencephalic or mid-brain root—of the trigeminal nerve. Below it is the main motor nucleus (4, fig. 219) of the trigeminal, and to the outside of this (above and somewhat laterally) is the main sensory nucleus. The other conspicuous objects in the dorsal (or tegmental) part of the section are the superior olivary nucleus (15), the trapezoid body and medial lemniscus (13), the thalamo-olivary tract (14), and the medial longitudinal fasciculus.

The trigeminal nerve has the most remarkable of roots and nuclei. There are three nuclei : (1) the main motor ; (2) the mesencephalic nucleus ; and (3) the sensory nucleus.

The first, the motor nucleus, consists of stellate cells of the usual somatic type. It belongs to the same column of grey matter as the vagal, glosso-pharyngeal and facial somatic nuclei. Its fibres emerge in approximately the position in which the nucleus is placed and run to the muscles of mastication.

The mesencephalic nucleus we shall see in later section. It is at the extreme edge of the grey matter around the cerebral aqueduct of Sylvius. The fibres from this nucleus pass downwards and emerge with the trigeminal nerve in the pons. Their function is assumed to be motor, although the fibres cannot be traced past the semilunar (Gasserian) ganglion. If they be sensory, as some claim, the root is altogether anomalous. We expect sensory nerve fibres to have their trophic [1] nerve cells outside the central nervous system.

The main sensory nucleus of the trigeminal nerve is found half-way up the pons. It is the head of the column which we have called the substantia gelatinosa. The sensory fibres, when they enter the brain, bifurcate. Some of the collaterals make synapses at once in the main nucleus, the others pass down in the spinal tract of the fifth trigeminal nerve, which we have met again and again, and make their final synapses at different levels right the way down to the region of the

[1] See pp. 64 and 73.

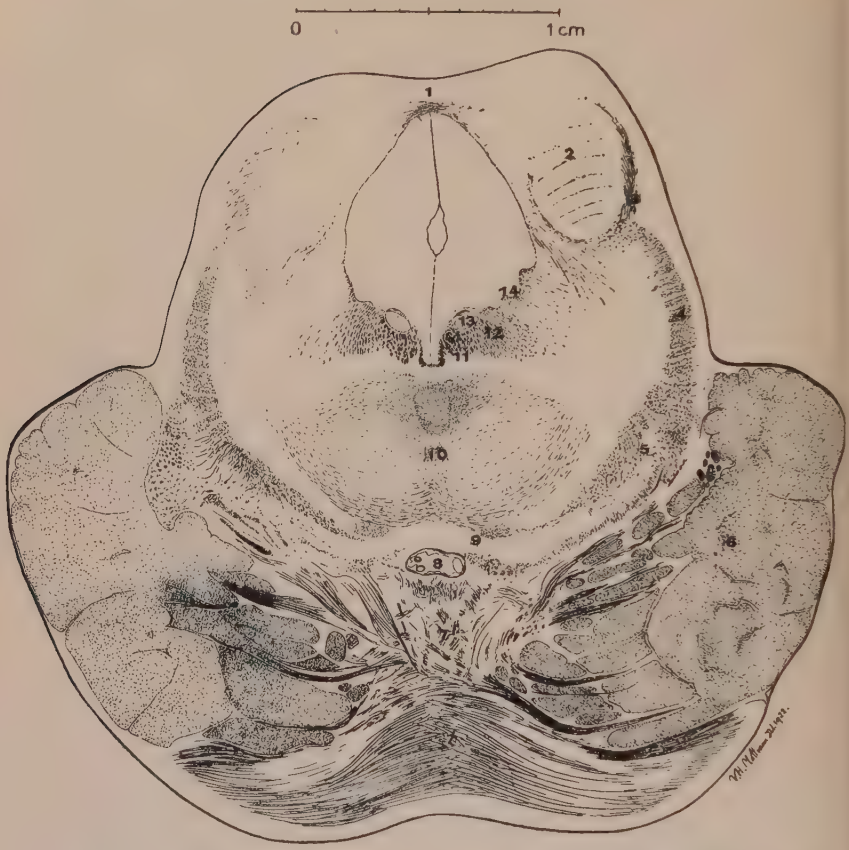



FIG. 221.—Transverse section of the mid-brain through the inferior colliculi (posterior corpora quadrigemina). × 3·5. G.A.H.

(Numerical order.)

1. Commissure of the inferior colliculi. 2. Nucleus of the inferior colliculus (posterior corpus quadrigeminum). 3. Fibres of the lateral lemniscus passing to the nucleus of 2. 4. Lateral lemniscus (or fillet). 5. Medial fillet. 6. Base of cerebral peduncle (pes pedunculi or crusta). 7. Decussating fibres of the pons. 8. Foramen cæcum. 9. Rubro-spinal (Monakow's) fasciculus. 10. Decussation of the brachia conjunctiva (superior cerebellar peduncles). 11. Medial longitudinal fasciculus (posterior longitudinal bundle). 12. Thalamo-olivary fasciculus. 13. Nucleus of the trochlear (fourth) nerve. 14. Descending (motor) tract of the trigeminal (fifth) nerve.

(Alphabetical order.)

Brachia conjunctiva, decussation of, 10. Colliculi, commissure of inferior, 1. Colliculus, nucleus of inferior, 2. Fillet, lateral, 4. Fillet, medial, 5. Foramen cæcum, 8. Lemniscus, fibres of lateral to inferior colliculus, 3. Lemniscus, lateral, 4. Medial longitudinal bundle, 11. Peduncle, base of cerebral, 6. Pes pedunculi or crusta, 6. Pons, decussating fibres of, 7. Posterior corpus quadrigeminum, 2. Posterior longitudinal bundle, 11. Rubro-spinal (Monakow's) fasciculus, 9. Superior cerebellar peduncles, decussation of, 10. Thalamo-olivary fasciculus, 12. Trigeminal nerve, descending, motor, tract of, 14. Trochlear nerve nucleus, 13.

second cervical nerve. The grey matter in which they end is the grey matter of the substantia gelatinosa, so that this nucleus extends from the cervical region of the spinal cord, through the medulla up to half-way through the pons, while the mesencephalic nucleus extends upwards into the mid-brain. Such a widespread distribution of the nuclei of a nerve is unique.

When we pass into the region of the inferior colliculi (posterior corpora quadrigemina) the appearance of things is much simplified (fig. 220). The division into two parts seen in the regions just below is still maintained. Below, in the basal part, we still see longitudinally running fasciculi (cerebrospinal and cortico-pontine fibres), the grey matter (nuclei pontis) and the transverse fibres of the pons. We cannot follow the latter up into the cerebellum, because they are splayed out forwards, and pass backwards towards their entrance into the cerebellum, the middle peduncle.

Above, in the tegmental region, we note first of all that the fourth ventricle has narrowed and passed into the cerebral aqueduct of Sylvius. Around this is the usual grey matter. Above are two rounded hillocks, the inferior colliculi. These consist mainly of grey matter, somewhat circumscribed, especially in higher sections (e.g. fig. 221), with white fibres from the lateral portions of the lemniscus.

The lemnisci have moved in position considerably since the last section given. They have been joined by fibres of the spinothalamic tract, and the projection fibres of cranial sensory nuclei (gustatory, auditory, and trigeminal), and have moved so that they can distribute themselves according to the functions of their component parts. Each lemniscus has become a boomerang-shaped object, with its thickest part at the angle which is placed immediately above the outer edge of the junction of the tegmental and basal parts of the section. The two parts receive the names of lateral and medial lemnisci or fillets. *The fibres in the lateral fillets are on their way to the colliculi* or corpora quadrigemina. Those on their way to the inferior colliculi are interrupted by the nuclei of the lateral fillet (2, fig. 220). Embraced by the two arms of the lemnisci are two conspicuous masses of decussating white matter, the brachia conjunctiva (or superior cerebellar peduncles). These we have seen in two previous sections. At first they form part of the roof of the fourth ventricle (figs. 218 and 219), then they pass down in a spiral direction

into the tegmentum, and, finally, reaching the middle line, decussate and pass to the red nucleus (see figs. 221 and 222).

Three other objects in the neighbourhood of the central grey matter are noteworthy:

(i) The emerging roots of the trochlear nerve. These consist of two very sharply defined bundles of white matter seen in different positions according to the exact level of the

FIG. 222.—Transverse section of the mid-brain through the superior colliculi (anterior corpora quadrigemina). × 2·9. G.A.H.

(Numerical order.)

1. Superior colliculus (anterior corpus quadrigeminum). 2. Stratum opticum. 3. Stratum lemnisci. 4. Stratum profundum. 5. Tecto-spinal tract and lateral lemniscus (fillet). 6. Brachium of inferior colliculus. 7. Medial geniculate body. 8, 8. Base of cerebral peduncle (pes pedunculi or crusta). 9, 9. Emerging roots of the oculo-motor (third) nerve. 10, 10. Substantia nigra. 11. Medial lemniscus (fillet). 12. Red nucleus with roots of oculo-motor nerve passing through it. 13. Rubro-spinal fasciculus (Monakow's tract). 14. Ventral decussation of tegmentum (Forel). 15. Fountain decussation of the tegmentum (Meynert). 16. Median longitudinal fasciculus (posterior longitudinal bundle). 17, 17. Nuclei of oculo-motor (third) nerve. 18. Cerebral aqueduct (of Sylvius).

(Alphabetical order.)

Anterior corpus quadrigeminum, 1. Aqueduct, cerebral, of Sylvius, 18. Colliculus, brachium of inferior, 6. Colliculus, superior, 1. Fillet, lateral, 5. Fillet, medial, 11. Geniculate body, medial, 7. Lemniscus, lateral, 5. Lemniscus, medial, 11. Medial longitudinal fasciculus, 16. Oculo-motor nerve, emerging roots, 9; nuclei of, 17; roots of, 12. Peduncle, base of cerebral, 8. Pes pedunculi or crusta, 8. Posterior longitudinal bundle, 16. Red nucleus, 12. Rubro-spinal (Monakow's) fasciculus, 13. Stratum lemnisci of superior colliculus, 3. Stratum opticum, 2. Stratum profundum, 4. Substantia nigra, 10. Tecto-spinal fasciculus, 5. Tegmentum, fountain decussation of (Meynert's), 15. Ventral (Forel's) decussation in tegmentum, 14.

section (fig. 220, 9). If they are near their nuclei (which are to be seen in fig. 221), or absent, the section is about halfway along the inferior colliculi. The lower the section is the further round they are towards the roof of the aqueduct. They decussate in the roof of the fourth ventricle, so that they have passed spirally backwards from their nuclei.

(ii) The medial longitudinal bundle, which is highly developed at this region (fig. 220, 7, and fig. 221, 11).

(iii) The mesencephalic root of the trigeminal nerve. This is seen at the extremest edge of the grey matter around the aqueduct, forming a small, slender crescentic object (fig. 220, 10).

Functionally considered, the various structures are as follows:

The basal portion. The longitudinal fibres carry impulses from the motor cortex to the motor nuclei of brain and spinal cord. Along with them are fibres to the cerebellum to enable it to guide muscle contractions initiated by the first set of fibres. They pass into grey matter in the pons, from the nerve cells of which axons pass across the raphe and up to the cortex of the cerebellum of the opposite side.

The tegmental portion. The lemnisci carry sensory impulses. Many fibres of the lateral lemnisci run to the inferior colliculi. Most pass into the nucleus of the inferior colliculi on the external and internal aspects of the nucleus (fig. 221). But some cross to the opposite side (fig. 221, 1). The fibres of the lateral fillet to a large extent arise from central connexions of the cochlear nerve. The inferior colliculi degenerate if the cochleæ in a young animal are destroyed. Clearly the inferior colliculi are closely connected with hearing.

The brachia conjunctiva carry impulses arising from the nuclei dentati of the cerebellum forward to the red nuclei of the opposite side, and also on to the thalamus. It can hardly be doubted that their function is to carry impulses that guide and control skeletal reflexes initiated in the mesencephalic and thalamic regions. The brachia conjunctiva are accompanied by fibres which carry impulses to the cerebellum from the spinal cord. They are the fibres of the anterior spinocerebellar tract of Gowers.

The trochlear nerve innervates the superior oblique muscle of the eyeball. Of the medial longitudinal fasciculus we shall speak later.

In the region of the superior colliculi (anterior corpora

quadrigemina) the brain is expanded laterally and is not so deep vertically. In the basal portion the two bases of the cerebral peduncles (which consist of cerebro-spinal fibres in the central three-fifths, and cerebro-pontine fibres for the remainder) are separating as we pass upwards. There is already (fig. 222) a very obvious furrow between them. Immediately above them we see a broad strand of grey matter, the substantia nigra, dark owing to pigmented nerve cells in its substance.

In the tegmentum two spherical nuclei are striking objects. These are the red nuclei. They contain numerous fibres in the lower sections, but many fewer higher up. These nuclei are placed on the path of the brachia conjunctiva, and the fibres of the latter undoubtedly end around cells in the red nuclei. The red nuclei also receive fibres from the cerebral cortex and from the corpus striatum. They emit fibres to the thalamus upwards and to the spinal cord downwards. The latter form the rubro-spinal tract of which we have already spoken. In fig. 222 the origin of the rubro-spinal tract is seen. There is a decussation of fibres from the two red nuclei and the development of a longitudinal bundle of fibres on each side passing downwards (fig. 222, 13, and fig. 221, 9).

On the outer sides of the two red nuclei the wings of the two lemnisci arise. The medial lemnisci are to continue on to the thalamus. The lateral lemnisci are shown in part going to the colliculi, and in part to the medial geniculate bodies.

In the grey matter around the aqueduct are prominent nuclei. These are the nuclei (somatic and splanchnic) of the nerves to the intrinsic and extrinsic muscles of the eye (i.e. ciliary, pupilo-motor, and superior, inferior and medial rectus muscles). From the oculo-motor nuclei the fibres run in a number of arcs, often taking a short cut through the red nuclei, and emerge in the furrow between the two bases of the cerebral peduncles. Close to this grey matter we find (1) the medial longitudinal fasciculus extending in a V around the lower part of the central grey matter, and (2) the mesencephalic root of the trigeminal nerve at the upper ends of the V. Below the point of the V is a second decussation, the fountain decussation of Meynert. This apparently arises from cells deep in the superior colliculi, and after the decussation gives rise to a longitudinal bundle in close apposition to the medial longitudinal bundle.

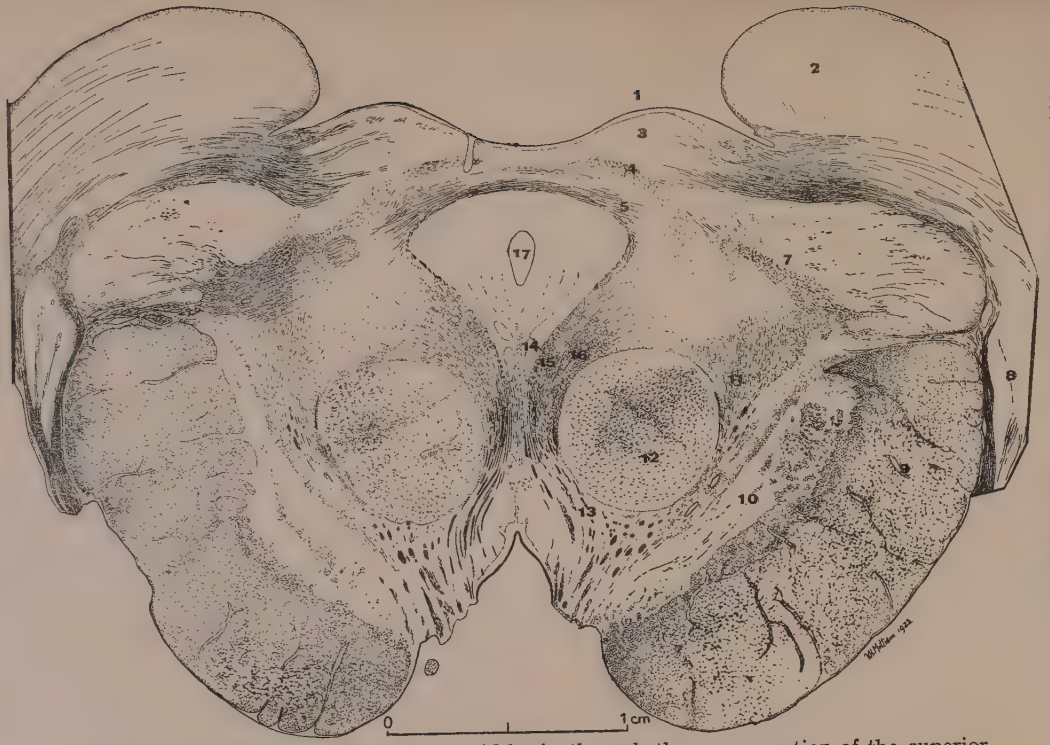



FIG. 223.—Transverse section of the mid-brain through the upper portion of the superior colliculi (anterior corpora quadrigemina). × 3·2. G.A.H.

(Numerical order.)

1. Superior colliculus (anterior corpus quadrigeminum). 2. Pulvinar of the optic thalamus. 3. Stratum opticum of superior colliculus. 4. Stratum lemnisci. 5. Stratum profundum. 6. Brachium conjunctivum of superior colliculus (to lateral geniculate body). 7. Brachium conjunctivum of inferior colliculus (to medial geniculate body) and medial geniculate body. 8. Lateral (external) geniculate body and optic tract. 9. Base of cerebral peduncle (pes pedunculi, crusta, or crus cerebri). 10. Substantia nigra. 11. Medial fillet. 12. Red nucleus. 13. Emerging fibres of oculo-motor (third) nerve. 14. Nuclei of oculo-motor (third) nerve. 15. Median longitudinal fasciculus (posterior longitudinal bundle). 16. Thalamo-olivary tract. 17. Cerebral aqueduct (of Sylvius).

(Alphabetical order.)

Anterior corpus quadrigeminum, 1. Aqueduct, cerebral, of Sylvius, 17. Brachium conjunctivum of inferior colliculus, 7. Brachium conjunctivum of superior colliculus, 6. Colliculus, superior, 1. Fillet, medial, 11. Geniculate body, lateral (external), 8. Medial longitudinal fasciculus, 15. Oculo-motor nerve, emerging fibres of, 13, and nuclei of, 14. Optic tract (and lateral geniculate body), 8. Peduncle, base of cerebral, or pes pedunculi or crusta, 9. Pulvinar of optic thalamus, 2. Red nucleus, 12. Stratum lemnisci of superior colliculus, 4. Stratum opticum, 3. Stratum profundum, 5. Substantia nigra, 10. Thalamo-olivary tract, 16.

Above the central grey matter are the two superior colliculi. These consist of different strata of white and grey matter. The stratum opticum contains fibres coming from the retinæ or going to the visual centre in the occipital cortex. The stratum lemnisci is deeper and makes connexion with fibres of the lateral lemniscus.

According to the level at which the section is cut, we may see two or three additional masses of grey matter. These are the medial geniculate body (figs. 222, 7, and 223), the pulvinar of the optic thalamus (fig. 223, 2), and the lateral geniculate body (fig. 223, 8).

The medial geniculate body is placed forward of the *inferior* colliculus, to which physiologically it may be said to belong, and anatomically is connected with it by means of a brachium (fig. 222, 6). The lateral geniculate body bears the same relation to the *superior colliculus*. They are two laminated masses of grey matter, the lamination being due to penetration by parallel layers of white matter.

In fig. 222 fibres from the lateral lemniscus and from the inferior colliculus (via the brachium of the inferior colliculus) are seen going to the medial geniculate body. In fig. 223, fibres from the optic tract and from the superior colliculus are seen passing to the lateral geniculate body. The pulvinar is the posterior extremity of the optic thalamus, and overhangs the brachia of the colliculi. It is intimately associated with the optic tract.

The microscopic anatomy of these parts and their connexions throw considerable light on their functions.

The medial longitudinal fasciculus reaches its maximal development in this region. It runs from the mid-brain close to the central line and immediately under the grey matter under the floor of the aqueduct and fourth ventricle, through the medulla, and becomes merged in the spinal cord with anterior ground bundle. That it is a tract of great importance is shown by the fact that its fibres obtain their myelin sheath early in fœtal life. In lower vertebrates it is one of the largest of tracts in the medulla. It receives fibres from the superior colliculi and from the vestibular nuclei. The latter run both up and down the central nervous system. Collaterals from the fibres enter the oculo-motor, the trochlear, and the abducens nuclei. The superior colliculi are connected with the retina. It is therefore reasonable to suppose that the medial

longitudinal fasciculus has the function of co-ordinating the movements of the eyes and the muscles of the neck and body in their responses to stimuli, either visual or vestibular.

The red nucleus, linked by afferent fibres with the nucleus dendatus of the cerebellum, the corpus striatum and the cerebral cortex, and by efferent fibres to the thalamus and to the motor cells of the spinal cord, evidently forms a reflex centre for some kind of muscular activity. It has been thought to be responsible for the anti-gravitational tonus of decerebrate rigidity.

The superior colliculi have to do with sensory impulses passing along the fillet, and, through neurones intercalated between the collicular grey matter and the oculo-motor nuclei, influence eye movements. Further, the colliculi are closely concerned with impulses from the retina. These influence, via the oculo-motor nerves, the reactions of the pupils and movements of the eyes. It is difficult not to believe that some cochlear nuclei projection fibres travel via the lemnisci to the superior colliculi, through these to influence the eye muscles, on the same plan as nerve fibres from the superior olivary nucleus (influenced by the cochlear nuclei) proceed to the nucleus innervating the lateral rectus muscles. So far there is no evidence for these fibres.

As stated above, destruction of the cochlea in the young causes atrophy of the inferior colliculi; destruction of the optic nerves, the superior colliculi.

The medial geniculate body, receiving fibres from the inferior colliculus through its brachium, and also directly from the lateral lemniscus, has to do with hearing. Fibres from the cochlear nuclei can be directly traced to the medial geniculate body. The lateral geniculate body and the pulvinar of the optic thalamus are in close relation to the optic tract. From them, as well as from the superior colliculi, fibres pass up to the occipital or visual cortex. Clearly these nuclei have to do with vision.

This completes the usual survey, from a histological point of view, of the central nervous system, except for the study of the cortices of cerebellum and cerebrum. In both of these the grey matter is external to the white. A section through the cerebellum shows it to have deep and ramified sulci, so that it appears foliate, feathery, or branched. Hence comes the

name "arbor vitæ" or tree of life. Over the whole of the cerebellum there is a continuous layer of grey matter, the cortex, and within this a central lamina of white matter—see figs. 217 and 219—in which small convolutions of the cerebellum are shown. The central white masses of the laminæ unite to form a central white mass, much larger than those which pass into the convolutions. In this central white mass, near the roof of the fourth ventricle, are found several nuclei of grey matter, the most conspicuous of which is the wavy nucleus dentatus, reminiscent of the inferior olivary nucleus, and shown in part in fig. 215. Other nuclei are the nucleus tecti, the nucleus emboliformus, and the nucleus globosus. These are found in the vermis.

When we look at the grey matter of the cortex of the cerebellum, we see that it is sharply differentiated with two layers, an outer, or molecular layer, and an inner or granular layer (fig. 59). At the margin of the latter, underneath the outer layer, is a row of very large cells, first discovered by Purkinje. These Purkinje cells are flask-shaped, with the neck towards the surface. Centrally there runs an axon passing into the white matter in the centre of the folium. From the upper neck-shaped portion spring a pair or more of branches, upon which the ramifications, disposed mainly in one plane, extraordinarily outdistance any other ramifications met with in the nervous system.

In a normal hæmatoxylin preparation, such as that from which fig. 59 was drawn, these ramifications are not seen. They need the Golgi process to make them obvious.

In the molecular layer the cells are not numerous. They are found in the deeper part. Their dendrons run inwards and form a dense basket-work around the cells of Purkinje. The "molecular" appearance of this layer is due to the multiplicity of axons in it cut transversely.

In the granular layer there is a mass of closely packed granular bodies. These are nerve cells with axons that pass outwards into the molecular layer, and then branch at right-angles up and down the folium and make connexions with the Purkinje cell dendrons of different levels.

The cerebral hemisphere shows no such foliation of its convolutions as is seen in the cerebellum, and under the microscope there is no such distinct stratification. The grey matter, the cortex, is a continuous sheath over the white matter

FIG. 224.—Cerebral cortex (stained with methylene blue). $\frac{2}{3}'' \times 1$. W.M.C.

1. Superficial plexiform layer. 2. Small pyramid cells. 3. Medium pyramid cells. 4. Superficial large pyramid cell layer, in which, however, are many medium-sized cells. 5. Layer of small stellate cells. 6. Deep layer of very large pyramidal (Betz) cells and medium-sized cells. 7. Small cells. 8. White matter (nerve fibres).

which is found internally to it. The general arrangement of the grey matter is into six or seven not very well-defined layers (fig. 224). Externally there is a plexiform layer consisting of horizontally disposed nerve cells with long dendrons passing for the most part horizontally too. Next come three layers of pyramidal cells of increasing size. The pyramidal cell has its base towards the white matter and its apex towards the surface. From the apex springs a dendron (see fig. 62), covered with prickles in a Golgi preparation, which passes up towards the plexiform layer and makes its synapses there. From the base axons pass in a centripetal direction. Below this layer there is usually a layer of granular cells, and then another layer of large pyramidal cells. If the section is taken from the motor cortex (precentral gyrus) the giant pyramidal cells of Betz are to be seen. Below this sixth layer is a layer of polymorphous or stellate cells, and then we reach white matter. In sensory areas (particularly in the visual and auditory areas) the layers of small cells (granules) are well developed, and give to the naked eye the appearance of white striæ in the grey matter. These lines are called the bands of Ballarger (or Gennari in the visual cortex). Around these small "granule" cells, the terminations of the fibres from the thalamus form their synapses. Betz giant cells are absent from the sensory areas, for their axons form the cerebro-spinal fasciculus and the nerve cells suffer Nissl degeneration when the nerves to the muscles on the cerebro-spinal fasciculi are damaged. Their function is clearly motor.

# NOTES TO THE STUDENT

1. Histology is essential to the study of physiology and pathology. The shape of the machine helps you to understand how it works. To know the abnormal, you must know the normal. Overdriven pathologists cannot spare the time to teach the appearance of the normal, which should be learnt before the student enters the pathology school. E.g. cancer cells originate in normal cells and breed approximately true to type. They migrate in the lymph channels and start second growths elsewhere in an entirely different tissue. How are these secondary growths to be recognized for what they are by the student if he cannot recognize the original tissue from which they sprang?

2. Much of the staining will be left to the student. Unless he masters the technique of staining and mounting early, he will never learn any histology. The reasons for staining and dehydrating given on pp. 281 et seq. must be understood and the methods practised. Nothing definite can be seen in a section if the paraffin is not removed, or if it is full of water when mounted in balsam, or full of xylol when mounted in a watery medium. [Such mistakes are common enough, as any examiner will testify.]

3. The best way to learn what a tissue is like is to draw it. Draw it at least twice the size you see it, because objects always look smaller when seen through a tube. The majority of the drawings in this book are exactly the size of the images at the level of the microscope table. They will appear at least twice as large as what you think you see them to be. (Best, then, when using them, to put a higher eyepiece on than the one used by the author, and draw considerably larger.) Use a sharp H or HH pencil and smooth, unlined paper. Draw the outlines of the cells and the nuclei and do *not* shade. *Make every line you use mean something.* Colour is of little use, unless it matches the stain, and the best coloured pencils only should be used. Five only will be sufficient: violet for hæmatoxylin, cerise for eosin, yellow for picric acid, magenta for acid fuchsin, and prussian blue for methylene blue.

4. The early part of your work, the recognition of elementary tissues, is the most important and the one most shirked. The more interesting part to the student is the "spotting" of sections. But you cannot do this "detective" work without mastering the elementary details. General appearance is of little use. It is

a regrettable fact that general appearances used, in the author's experience, to lead students to confuse the mammary gland, the thyroid gland, the prostate gland, and the lung each with the other! No one who knew what an elementary tissue, such as an epithelium or an unstriped muscle cell, looked like, could make such mistakes. You must know your elementary tissues before you can "identify specimens."

5. So long as examiners ask you to identify specimens, you will think it your main object in histology. It is best to import the detective method (i.e. deductive) into your process of identification. E.g.: The section is ring-shaped and has a star-shaped lumen in the middle. It is some hollow organ such as the uterus, or some part of the alimentary tract. Is it œsophagus or what? There are two layers of muscle in the thick muscular coat. The epithelium of the mucous membrane has no projections from it when seen under the low power. This rules out the small intestine. Under the same power the epithelium is seen not to be stratified. This rules out œsophagus, leaving only large intestine and uterus as the main possibilities. The nature of the epithelium, the glands of the mucous membrane, the position of one of the coats of muscle, whether directly under the mucous membrane, or whether separated from it by a submucous coat, will determine which of these it is.

6. Histology is not difficult, it merely has endless detail and is tedious. Anyone can master histology who has patience and perseverance. It will be of the greatest use to the student if he will master it early in his career, and remember not to forget it.

## MOUNTING AND STAINING SECTIONS

The Reason for Mounting—Specimens are mounted in some medium which solidifies, or at any rate gelatinizes, to make them permanent. They are mounted in substances having the same refractive index as they have themselves, or are so soaked in these substances that there are no sudden large changes of refractive index as you pass from medium to tissue. Otherwise there would be unpleasant fringes and rings round the section and its parts.

The Reason for Staining—If tissues are thoroughly soaked in such media, they become almost invisible. They must be coloured. (A transparent white glass rod is invisible in cedar-wood oil and balsam, but a coloured one is not.) They are coloured or stained in several ways, of which *dyeing* is for the student the most used.

The Methods of Staining—(1) *Dyeing*. Practically all staining of preparations comes under this heading; all the rest are special processes for special purposes. Dyes can be divided into two types: (*a*) those like hæmatoxylin and carmine, which stain slowly and are deposited preferentially in parts of the cell, such as the chromatin of the nucleus; (*b*) the aniline dyes, which stain the whole cell

rapidly, but can be washed out differentially, leaving the stain in the chromatin, or in special granules, etc.

A further classification of dyes is into (*a*) nuclear [1]; (*b*) cytoplasm or cell-body dyes. They correspond roughly to basic and acidic dyes. Dyes are often salts, and the colour-bearing part of the stain may take the place either of the metal in a salt or of the acid radicle. Basic fuchsin has the colour nucleus in the place of the metal, acid fuchsin in the place of the acid radicle. Basic fuchsin stains nuclei, acid fuchsin stains the rest of the cell.

| Nuclear stains are: | Cytoplasm stains are: |
|---|---|
| Hæmatoxylin. | Acid fuchsin. |
| Carmine. | Eosin. |
| Methylene blue. | Light green. |
| Methyl violet. | Picric acid. |
| Basic fuchsin. | |

The simplest technique of staining is the following. There is nothing better for the ordinary section than:

(*a*) Hæmatoxylin, followed by

(*b*) Eosin or Biebrich scarlet as the counter or contrast stain.

A. *The section is given to you cut in paraffin wax.* Before it can be stained it must be stuck on a slide, the paraffin washed out of it by xylol, and the xylol washed out of it by a substance that will mix with the fluid in which hæmatoxylin is made up. Unfortunately, stains work best in watery or alcoholic solution, and neither of these dissolve, or dissolve in, paraffin. Consequently all paraffin must be first removed. Hence the array of xylol, carbol xylol, absolute alcohol, 95 per cent. alcohol, 75 per cent. and 50 per cent. alcohols.

MOUNTING—

(i) Cover the slide with a very thin film of "fixative." (A drop the size of a pin's head spread well over the slide is sufficient.)

(ii) Drop a drop of water about the size of a shilling on it.

(iii) Float one section on the top of this. (Sections can be picked up by means of a needle or dry paint-brush.)

(iv) Warm over a small flame till you can only just bear your knuckle on the under-side of the slide. The section flattens. *The paraffin must not melt.*

(v) Tilt the slide gently, holding one edge of the preparation with a needle against the slide. Allow the water to drip off, and stand the slide vertically for a little time to drain. If in a hurry, lay flat and blot section with fluffless blotting paper, and press section gently down into the fixative. Leave as long as you can to dry.

[1] Nuclear stains *do* stain the cytoplasm, but more faintly than the nuclei.

(vi) Warm to melt the paraffin, but do not do more than this.

(vii) Plunge the slide into xylol, or drop xylol from a dropping bottle on to the section. Gently wave the slide in the xylol or see-saw it about in your hand for a minute, dropping two lots more of xylol on and running off the excess. *Never allow your slide to dry at or after this stage.* The xylol dissolves the paraffin.

(viii) Blot off excess xylol, but do not touch the section or let it dry, and drop on absolute alcohol. (Or pass through the alcohols.) The alcohol removes the xylol.

(ix) Repeat with 70 or 75 per cent. alcohol, and, if provided, 50 per cent.

(x) Plunge into a deep dish of distilled water and move it gently to and fro.

The slide is now ready for staining. (This long process is the essential preliminary for most methods of staining, though, of course, if a stain made up in 70 per cent. alcohol is used as the first or only stain it is *not* necessary to take the preparation down to distilled water. Seventy per cent. will be the stopping-place.)

STAINING—

(i) Remove excess of water. Drop a few drops of the stain (hæmatoxylin) on the section, and see-saw to and fro for a minute. Wash off the stain in distilled water. It will probably be a faint purple and not yet deep enough. Drop another drop of the stain on and repeat. If it is now a medium purple in tint, this is enough. Judgment is the only way of telling. Some tissues take much longer than others.

(ii) Wash thoroughly in distilled water and transfer to tap water. This, after a minute or so, turns the hæmatoxylin blue. (Presumably a hæmatoxylin "lake" is formed.)

(iii) Blot round the edges, and then, if the counter stain is made up in 70 per cent. alcohol, drop 70 per cent. alcohol on the section. (If in a hurry, omit this.)

iv) Drop a drop or so of the counter stain on the preparation. Judgment alone will tell you when it has been on long enough. With eosin, try it after thirty seconds, i.e. wash in 70 per cent. alcohol and look at the slide either with naked eye or on the stage of the microscope. Parts of the slide should be pink to red, but not vividly so. (With Biebrich scarlet, which is a watery stain, cover the slide with a watch glass and do something else for fifteen minutes. Then try as with eosin, but wash in water and not alcohol.)

(v) Wash the slide thoroughly with 70 or 75 per cent. alcohol, then 95 per cent., then absolute alcohol, then three changes of xylol.[1] Blot off excess of xylol, drop one drop of Canada balsam on the preparation, and cover with a cover slip.

Traps for the beginner are:

(*a*) Not getting the paraffin out.

(*b*) Over or under staining.

(*c*) Not getting the water out by means of absolute alcohol before putting the section into xylol.

B. *The section is given to you in water, having been cut in gum.* Here an ultra-clean section lifter is almost essential, and watch glasses are used. Omit all the stages of mounting above and pass straight to staining. Use a very clean mounted needle (either new or very well scraped and polished) and transfer by its aid one or more sections to hæmatoxylin in a watch glass.

Examine at the end of a minute in distilled water.

If reasonably stained, wash well and transfer to tap water.

When "blued," transfer on needle to 50 and then to 70 or 75 per cent. alcohol.

Stain in eosin, examining as before. When stained, wash thoroughly in 75 per cent. alcohol.

Past this point use a section-lifter, and see that there are no creases in the section. Pass through 95 per cent. and absolute alcohol to xylol, or 95 per cent. alcohol to clove oil.

Float on to a slide. Mop up excess of xylol or clove oil, and cover.

A good alternative to hæmatoxylin and eosin is hæmatoxylin and van Gieson (which contains picric acid and acid fuchsin).

Stain rather deeply with hæmatoxylin and "blue" the preparation thoroughly.

Have ready a deep dish of water or the tap running.

Drop van Gieson on the slide and at the end of ten to fourteen seconds, wash it off rapidly.

Dehydrate and mount in balsam.

(Some prefer that the van Gieson should be washed off with alcohol to retain the picric acid stain. The above treatment retains enough, but the fuchsin is sometimes faint. If so, it can be reinforced by staining again with acid fuchsin alone. Too long in van Gieson turns the nuclei, which should be violet, an unpleasant brown.)

Van Gieson is an admirable stain where there is much muscle or elastic tissue in the presence of connective tissue.

(2) *Differential Solution.* This is used in staining fat with fat-

[1] Or one lot of carbol xylol and one of xylol. Carbol xylol is not much use with methylene blue or van Gieson.

soluble dyes (Sudan III, Scarlet R). These are more soluble in fat than in 70 per cent. alcohol. You treat the section or film (which must never have been in an alcohol of greater strength than 70 per cent., or of course in any fat solvent, e.g. xylol, chloroform, etc.) with a saturated solution of the dye, covered to prevent evaporation for at least twenty minutes. You *wash the section in water direct* and mount in glycerine, glycerine jelly, or Farrant's medium. (These must be used as mountants, for they mix with water. Balsam does not and therefore cannot be used.) The fat is stained because the dye prefers to dissolve in it rather than in 70 per cent. alcohol.

(3) *Impregnation.* Tissues can reduce compounds of silver, gold, platinum, osmium, etc., to the respective metals or lower oxides. These are precipitated in the cells and show dark under the microscope. Osmic acid for fat, silver nitrate for cement substance between cells, gold for nerve-endings, Golgi preparations of nerve cells, etc., are examples.

The student may have to prepare a silver nitrate preparation of the epithelioid membrane of tendon, nerve, or mesentery.

(i) Gently stretch the membrane or object. (Do not use a fixative if you stretch the membrane over a slide or coverslip.)

(ii) Paint with 1 per cent. silver nitrate.

(iii) After not more than one minute wash in isotonic sodium sulphate solution and place it in the brightest daylight (sunlight preferable) obtainable for half an hour. Dehydrate (i.e. pass up the alcohols) to xylol and mount in balsam.

(4) *Chemical Precipitation.* This method does not concern the average student much. A good example is the test for iron. Sections cut frozen in gum are warmed gently with very dilute hydrochloric acid. This sets free iron. The addition of potassium ferrocyanide gives a blue precipitate on the iron. Sections can be counterstained and dehydrated. Silver salts are used for chlorides and sodium cobalti nitrite for potassium.

## PREPARATIONS FROM FRESH TISSUES

There are a few preparations from fresh tissues with which the student should familiarize himself.

1. Dry films. E.g. of marrow, grey matter of central nervous system, spleen, pus, sputum, blood, urinary sediment.

These are important in medicine as well as in histology.

A clean slide is taken, a small amount of the substance to be examined—about a pin's head in size—is spread by means of a clean flamed needle, or scalpel handle, on the slide, and the film dried. Waving in the air hastens the drying. Then the back of the slide is warmed gently till it is about to hurt the knuckle when placed against it. (N.B.—Films must not be cooked.) The film is then ready for staining.

Methylene blue is usually good enough for staining purposes. Drop on a few drops of Löffler's methylene blue or a strong watery solution with a minute amount of caustic soda in it. Leave for one minute unless there are many nuclei present, when twenty seconds will be enough. Wash thoroughly in water under the tap. Blot dry. Leave to dry in the air for a few minutes. Mount *direct* in balsam without using any intermediate alcohols, etc.

Many bacteriological methods are variants of this, e.g. Ziehl-Neelsen stain for bacillus tuberculosis.

Blood films need ultra-clean slides and coverslips and are stained in a special stain, a methylene blue eosinate.

The slides are prepared beforehand by dropping each separately into hot bichromate of soda to which sulphuric acid has been added. Then each is washed separately in tap-water, dropped separately into distilled, and then separately into 95 per cent. alcohol or absolute, or a mixture of alcohol and ether, and stored in it. The coverslips are treated the same way. When wanted one is taken and put into a flame to burn the alcohol and then allowed to cool.

A small drop of blood is placed near one end of a clean slide. By means of another, held at about 60° to the first, it is *dragged* along towards the far end rapidly and regularly as far as it will go. This leaves a thin, regular film behind, which should dry at once. It may be helped to dry on muggy days by waving it in the air. (The stain will fix it.) Should the slide be in the least greasy lagoons surrounded by corpuscles will be seen. Such a film should be discarded.

Drop five drops of Leishman's stain on the film. Leave for one minute.

Drop five drops of distilled water into the stain. Leave for five minutes.

Wash thoroughly in at least 50 c.c. distilled water to which a few drops of stain have been added, till the film looks rose pink to the naked eye and until under the microscope the lobes of the polymorphonuclear leucocyte nuclei are clear-cut. Blot dry and leave for a few minutes. Such a slide is usually examined without a coverslip under the $\frac{1}{12}$ in. in cedar-wood oil. Preparations keep best when *not* mounted in balsam.

2. Moist films. E.g. of subcutaneous areolar tissue, mesentery, pia mater, frog's bladder. A small portion of the tissue or one horn of the bladder is taken and placed on a clean dry slide. By means of two clean mounted needles it is spread out (the bladder must be inside uppermost). Its own serous fluid is enough to stick it to the slide. Most tissues will spread ten times as far as might be expected —the mesentery being an exception.

When spread and beginning to dry the film is fixed, unless it be of frog's bladder. (*Then* the epithelium must be removed before

fixation from the inner surface of the bladder by rubbing with the finger-tip moistened, if need be, with a tiny amount of saliva.)

If for ordinary staining, the film is fixed by pouring on 95 per cent. alcohol and leaving it for five minutes. It is then treated as if it were a section mounted on a slide—i.e. run down the alcohols, stained with hæmatoxylin, up to 70 per cent., stained in eosin, dehydrated and mounted in balsam.

Or it may be stained in methylene blue and treated either as a dry film after washing or rushed through the alcohols rather rapidly to xylol and mounted in balsam. (This is useful for connective-tissue corpuscles.)

If it is to be stained for fat the film is fixed with 10 per cent. formalin (five minutes), then placed in 70 per cent. alcohol, then Sudan III in 70 per cent. alcohol for at least ten minutes (better half an hour), *washed in water* (best in a deep dish), and mounted in Farrant's medium. (This medium consists of glycerin and gum and so mixes with water.)

3. Teased preparations. E.g. nerve, muscle, tendon, glands.

Nerve. Take half an inch. Hold down one end of it with the scalpel handle on the slide, and by means of a needle spread the other out fan-wise by dragging a clean needle through it again and again. It is difficult to tease it too much. Two methods of fixation are used:

(*a*) Place osmic acid ($\frac{1}{2}$ to 1 per cent.) on the teased nerve. Leave for half-hour. Wash. Mount in glycerin or Farrant, or dehydrate and mount in balsam.

(*b*) Fix in 95 per cent. or absolute alcohol, transfer to a mixture of ether and chloroform to dissolve the myelin sheath. Keep it moving in this. Transfer back to alcohol (95) and treat as a paraffin section—stain in hæmatoxylin and eosin.

Muscle. Tear one end of a tiny strip of muscle fibres from a skeletal muscle. Paint with 95 per cent. alcohol, keeping it stretched. Leave for a minute till it has become opaque. Transfer to a watch glass of 95 per cent. alcohol and leave for five minutes. Now stain with hæmatoxylin and eosin, or hæmatoxylin and van Gieson. Take up through the alcohols to clove oil or carbol xylol, place on slide and tease very thoroughly. Add a drop of balsam and cover.

Tendon. Tease as with nerve. Fix in 95 per cent. alcohol. Stain in hæmatoxylin and eosin.

Glands. It is difficult to make a permanent preparation of a teased gland. The cells are examined in the fluid in which they are teased (serum, or isotonic salt, or Ringer's solution). But a dry film can be made from the teased cells and stained either with methylene blue or hæmatoxylin and eosin.

The fresh tissues may be conveniently obtained from the following situations :—

Areolar tissue : between the skin and the body wall, thorax or abdomen, of a rat.

Mesentery : between the folds of the small intestine of a rat.

Pia mater : covering the brain and spinal cord of a rabbit or cat.

Unstriped muscle : on the ventral side of the lower end of the large intestine of a frog will be found the two-horned bladder, best recognized by the tortuous veins on the surface of that organ.

Nerve for silver nitrate : running internally from the mid-line just above the backbone of the frog to the loose skin above it.

Nerve for teasing : the sciatic of frog or rat.

Striped muscle : the sartorius of frog or rat. If for film preparation the sterno-cutaneous of the frog.

Tendon : on the underside of a frog's hind foot.

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